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PHENOLOGY AND GROWTH OF HAWAIIAN PLANTS, A PRELIMINARY REPORT

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ABSTRACT

Observations on phenology and growth of several Hawaiian plants between January 1971 and June 1972 are presented. Most species exhibit some seasonality in flowering, fruiting, flushing, and (at least in deciduous species) leaf fall. Most phenophases show single annual peaks, but durations of phenophases generally extend over periods of several months, and onset and cessation of most phenophases in gradual rather than sharply marked.

In *Acacia koa* the flowering peak occurred between December 1971 and February 1972 in plots on the Mauna Loa Strip Road, and in October 1971 in the Kilauea Forest Reserve, but all plots showed considerable winter flowering. However, little or no flowering took place in the winter of 1970-71. At higher elevations peak flushing was during summer months, at lower elevations during winter and spring.

In *Sophora chrysophylla* flowering and flushing took place throughout the year without pronounced peaks at Kipuka Nene. Plots at 6000 and 6700 feet on the Strip Road showed flowering throughout the year, but with pronounced winter peaks. At 4000 and 5150 feet on the Strip Road the flowering peak was during winter and no summer flowering was found. Peak flushing occurred during spring and summer in all Strip Road plots.

Cheirodendron trigynum shows peak flowering in summer, peak flushing in winter and spring. *Sapindus saponaria* flushes in spring, flowers in summer, and loses its leaves in winter. *Diospyros ferrea* flushes throughout the year, but most heavily in fall and winter; peak flowering is during winter and spring. *Erythrina sandwicensis* loses its leaves in spring, flowers during summer, and flushes in the fall. *Ilex anomala* flushes in spring, shows peak flowering in summer with flowering extending into fall and winter. *Coprosma ochracea* has peak flushing and flowering simultaneously in spring. *Myrsine lessertiana* has peak flushing in spring, with a less pronounced flush in fall; the flowering peak is

late winter, continuing through spring. *Myoporum sandwicense* shows peak flowering in summer and fall; flushing seems to occur throughout the year. *Santalum ellipticum* flowers and flushes throughout the year, with peaks for both extending from summer to fall. *Dodonaea viscosa* seems to flush throughout the year; peak flowering occurs in fall and extends into winter and spring.

All species examined show cambial activity throughout the year, but growth rates vary from month to month. It has not been possible to demonstrate correlations between rainfall and growth rates.

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INTRODUCTION

Phenology refers to the timing of biological events and their relationship to seasonal climatic changes. In general, phenological phenomena are more sharply defined and more easily observed in temperate areas with pronounced seasonal differences than in the humid tropics which have more uniform climatic patterns throughout the year. Still, a number of phenological studies of plants have been conducted in tropical areas (Baker and Baker, 1936; Coster, 1923, 1926; Daubenmire, 1972; Holttum, 1940; Koriba, 1958; McClure, 1966; Njoku, 1963; Pinto, 1970; Richards, 1964; among others). Such studies have yielded interesting information on the relationships between seasonal plant phenomena and climatic phenomena, and have also provided information on relationships among different organisms, such as fluctuations in animal populations related to production of fruits or flowers in certain plant species, or fluctuations in decomposer populations related to the increased litter accumulation at certain seasons when leaf fall is most pronounced.

In Hawaii very few phenological studies have been made of native or naturalized plants. Occasional notes on flowering or fruiting seasons have appeared in floristic works (Rock, 1913), and a few studies of phenology of cultivated and ornamental plants have been made (Lanner, 1966; Neal, 1965; Pearsall, 1951; Rasid, 1963). There are only three significant studies dealing with native species growing under natural conditions. Baldwin (1953) studied phenology of flowering in *Metrosideros collina* and *Sophora chrysophylla* in relationship to the seasonal cycles of Hawaiian honeycreepers on Kilauea and Mauna Loa. Lanner (1965) made studies of flowering, fruiting, and shoot growth of *Acacia koa* on Mauna Loa. Porter (1972) has just completed an intensive study of the phenology of *Metrosideros* on Oahu and Hawaii.

In addition to studies of flowering and fruiting, leaf production and leaf fall, another phenological phenomenon of interest to botanists is the seasonal activity of the vascular cambium. In areas with pronounced seasonal differences leading to periodic differences in rates of growth of the vascular cambium, and correlated differences in the sizes of the secondary xylem cells produced by the cambium, growth rings appear in the wood. Such rings, typically formed at the rate of one per year, allow reliable estimates to be made of the ages of trees. In the tropics, some species produce distinct growth rings in the wood at regular intervals, many species produce growth rings very irregularly or not at all (Chowdhury, 1939, 1940a, 1940b; Chowdhury and Ghosh, 1950; Chowdhury and Rao, 1949; Coster, 1925, 1927, 1928; Mariaux, 1967; Studhalter, 1955; Studhalter, et al., 1963).

In Hawaii most tree species which have been studied in detail do not produce regular growth rings in the wood (Brown, 1922; Lamberton, 1955; Lanner, 1966; Sastrapradja and Lamoureux, 1969). When growth rings are absent, or produced irregularly, it becomes difficult to estimate accurately the ages of trees. This presents problems for biologists who are interested in determining ages of individual trees or forest stands. It also presents problems for foresters who need information about ages and growth rates of trees in order to make appropriate decisions on forest management practices. Therefore we have been investigating the phenology of cambial activity in an attempt to learn if there are seasonal differences in growth rates even though distinct growth rings do not occur in the wood.

The studies reported here were conducted within the framework of the Island Ecosystems IRP, US/IBP since they were undertaken not only to assemble basic information on phenological phenomena and growth periodicity in native and naturalized Hawaiian plants, but also because it was anticipated that the results would be useful to those investigators concerned with periodic fluctuations in populations of consumers and decomposers, and to those people concerned with natural resource management.

DIFFICULTIES OF CONDUCTING PHENOLOGICAL STUDIES IN HAWAII

In Hawaii, although seasonal differences in climate do exist, they are usually not extreme differences. For example, diurnal fluctuations in temperature in any one location are usually greater than the annual fluctuation in mean monthly temperature for that area (Blumenstock and Price, 1967). While there are significant differences in average monthly rainfalls throughout the year, in most areas where this study was conducted the precipitation is not regularly so low as to be inhibitory to plant growth for significant periods of time. Therefore, in our study areas sharp seasonal differences which have obvious direct effects on plant phenological responses are not pronounced.

Most species which we have observed do exhibit distinct seasonal peaks in various phenophases. However, a careful search will frequently reveal that some individuals in a population will be flowering, or fruiting, or undergoing a flush of vegetative growth at any month of the year. In some species, different branches of the same plant will be exhibiting different phenophases at the same time. The beginnings and ends of particular phenophases in populations are usually not sharply marked. For these reasons, study of herbarium materials is not an appropriate means of determining times of flowering or fruiting in populations, since collectors typically preserve only fertile material.

Certain types of phenological observations essential for phenological studies in temperate areas, (e.g., date of appearance of first new leaf, date of opening of first flower), are not particularly meaningful under Hawaiian conditions. We find it necessary to use indices or percentages, (e.g., percentage of plants in flower on a particular date), to express our observations. On the other hand, given the relatively long periods of time involved in the onset, duration, and cessation of a particular phenophase in a given population, it is generally unnecessary to make the daily or semi-weekly observations which are required when phenophases are characterized by the rapid onset and short duration typical of shorter growing seasons. We have found that observations at monthly intervals are satisfactory in most instances under Hawaiian conditions.

Preliminary observations have indicated that the timing and duration of phenophases may differ from year to year in the same species. For example, Lanner (1965) found that in 1963-64 heavy flowering in Acacia koa at 4000 feet elevation on the Mauna Loa Strip Road occurred between early December and March, while at 6700 feet heavy flowering occurred between March and May. In 1971-72 we found that heavy flowering occurred between October and February at 4000 feet, and between December and April at 6700 feet. Also, at 6700 feet there was no flowering between January and November 1971. Such differences indicate that observations must be made over periods of several years before valid conclusions can be drawn. The need for observations extended over a period of several years is emphasized by the data on year-to-year variability in rainfall and drought periods presented by Blumenstock and Price (1967, pp. 10-11).

Therefore, this paper is offered only as a preliminary report. It summarizes the observations made during the first 18 months of the study, and the data presented should be of interest to other investigators. However, any conclusions about plant phenological phenomena which are presented must be considered as tentative ones. It is anticipated that after data have been obtained covering a three-to-five year period, it should be possible to present conclusions which have reasonable validity. In the meantime, it seems useful merely to present our results to date.

METHODS

Detailed observations have been made on plants growing in nine plots on the island of Hawaii (FIG. 1), one in the Kilauea Forest Reserve and eight in Hawaii

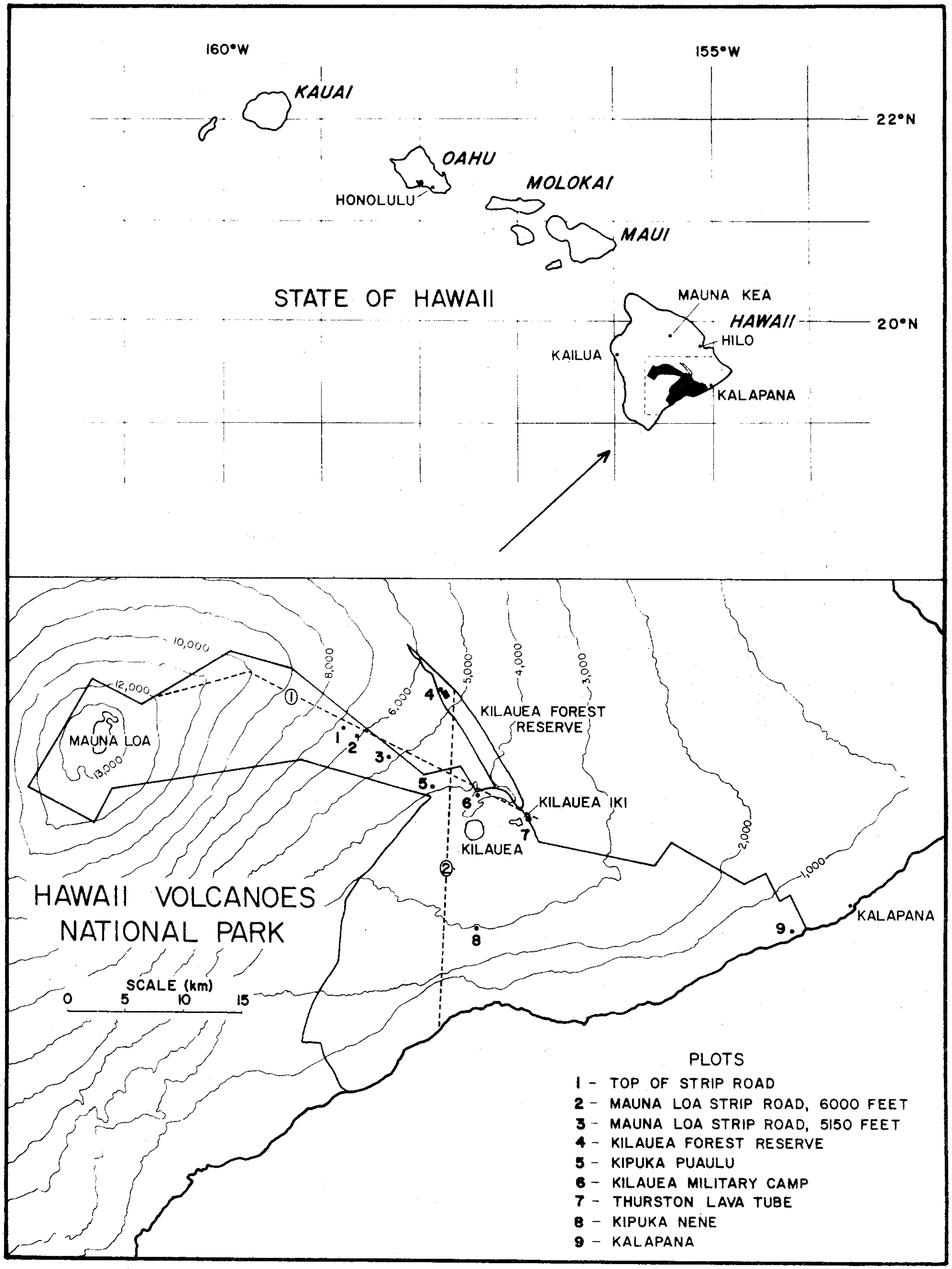


FIG. 1. Map of the Island of Hawaii showing location of study plots.

Volcanoes National Park, at elevations ranging between 8 m and 2040 m, in a variety of climates and vegetation types. TABLE 1 gives the locations and vegetation types of all plots.

Intensive studies

For 12 common tree species repeated observations at monthly intervals are made on ten marked individuals in each plot in which it occurs (TABLE 2). These observations include:

a) flowering - flower buds or flowers present, with indications of the quantity of each.

b) fruiting - young or mature fruits present, with indications of the quantity of each.

c) dispersal - dropping of fruits or seeds, with indications of quantity.

d) leaf fall - occurrence of recently fallen leaves under the tree, with indications of quantity.

e) vegetative flush - occurrence of conspicuous growth of new leaves and twigs, with indications of quantity.

f) vegetative - this term is used to indicate a plant in full leaf which is not flowering, fruiting, or undergoing vegetative flush.

g) circumference - the circumference, in mm, is measured. During 1971 this was accomplished by using a steel tape measure which was placed in the same position at each reading by using nails which remained in the tree. In early 1972 we started using simple dendrometers, made of aluminum tape held by small springs, which remain permanently in place on each tree.

h) cambial activity - each month a 1.5 cm cube of tissue containing inner bark, vascular cambium, and sapwood was removed from one tree of each species in each plot using a hammer and chisel. This block of tissue

TABLE 1. Locations and characteristics of plots in which phenological observations are being made.

Plot number	Name	Latitude (N)	Longitude (W)	Elevation (m)	Vegetation and climate type	Date of earliest observation
1	Mauna Loa Strip Road Top	19°30'	155°23'	2040	Open forest; summer dry with frequent low clouds	January 1971
2	Mauna Loa Strip Road 6000 feet	19°29'	155°22'	1830	Open forest; summer dry with frequent low clouds	November 1971
3	Mauna Loa Strip Road 5150 feet	19°28'	155°21'	1570	Open forest; summer dry with frequent low clouds	March 1971
4	Kilauea Forest Reserve	19°31'	155°18'	1650	Montane rainforest; humid	March 1971
5	Kipuka Puaulu	19°27'	155°19'	1220	Open to closed forest; summer dry with frequent low clouds	March 1971
6	Kilauea Military Camp	19°26'	155°17'	1220	Open forest with grasses; humid-summer dry transition	October 1971
7	Thurston Lava Tube	19°25'	155°15'	1220	Montane rainforest; humid	May 1971
8	Kipuka Nene	19°20'	155°15'	915	Open forest; summer dry	January 1971
9	Kalapana-Wahaula	19°20'	155°02'	8	Open forest; warm tropical, summer drought	March 1971

TABLE 2. Tree species on which intensive monthly observations are made on marked individuals, and the plots in which these observations are made.

SPECIES	FAMILY	PLOT NUMBER(S) (from TABLE 1)
Acacia koa	Mimosaceae	2, 3, 4, 5
Cheirodendron trigynum	Araliaceae	4
Coprosma ochracea	Rubiaceae	7
Diospyros ferrea	Ebenaceae	9
Dodonaea viscosa	Sapindaceae	3
Erythrina sandwicensis	Papilionaceae	9
Ilex anomala	Aquifoliaceae	7
Myoporum sandwicense	Myoporaceae	4
Myrsine lessertiana	Myrsinaceae	7
Santalum ellipticum var. *paniculatum*	Santalaceae	6
Sapindus saponaria	Sapindaceae	5
Sophora chrysophylla	Papilionaceae	1, 2, 3, 5, 8

was preserved in Craf III, and later embedded in celloidin and sectioned on a sliding microtome, after which the sections were stained and the extent of cambial activity determined by counting the numbers of immature cells in the cambial zone between the innermost mature phloem cells and the outermost mature xylem cells. Since this technique has not proved entirely satisfactory, because of mechanical damage to the cambial zone caused by removal of tissue from the tree, we have recently changed to the "pin-in-the-cambium" technique described by Wolter (1968). With this technique, each month a stainless steel pin is inserted through the bark into the cambium and left in place in the tree. The pin kills two or three cambial initials, thus leaving a trace in the wood of the location of the cambium at the time the pin was inserted. After six months a cylinder of bark, cambium, and wood is removed and processed for microscopic examination, which reveals the amount of growth the tree has undergone between the date the pin was inserted and the date the sample was collected.

i) branch mapping - five small branches (twigs) on one tree of each species in each plot were permanently marked. At each observation period the length of each twig is measured and the twig is mapped, with the location of each leaf, leaf scar, bud, flower, and fruit noted. This technique provides useful quantitative data and allows precise observations of such features as length of life of individual leaves or time required for fruit development.

Extensive studies

In each plot observations are made on the phenology of several other plant species in a less intensive way. The species studied, and the plots in which they occur are listed in TABLE 3. For each species observations are made on at least ten individuals per plot, except in a few cases where less than ten are present in the plot. However, the same individuals are not necessarily observed at each visit, as our objective in this part of the study is to determine the general phenology of the population in the plot rather than the phenology of certain individuals. The observations made on most species (see details under 1, above) include:

a) flowering

b) fruiting

c) dispersal

d) leaf fall

e) vegetative flush

f) vegetative

For annual species, or species which produce annual shoots from perennial rootstocks, the time of death of the annual parts is noted.

For ferns the phenophases recorded are:

a) frond production - the growth of new fronds

b) spore release - spores formed and disseminating

c) frond death - fronds dying or dropping

Quantification of data

Quantification of data on flowering, fruiting, dispersal, leaf fall, and vegetative flush presents certain problems related to differences in morphology of the species being studied. For certain species, (e.g., *Erythrina sandwicensis*, *Sophora chrysophylla*), it is usually feasible to count accurately the number of inflorescences present on a tree, while for other species, (e.g., *Acacia koa*, *Diospyros ferrea*, *Myoporum sandwicense*), it is impossible to count accurately total numbers of flowers or inflorescences. When feasible actual counts are recorded; in other cases estimates are made of the percentage of branches on a tree which are

TABLE 3. Species on which monthly observations are made on populations, and the plots in which these observations are made.

SPECIES	FAMILY	PLOT NUMBER(S) (from TABLE 1)
TREES		
Alphitonia ponderosa	Rhamnaceae	8
Canthium odoratum	Rubiaceae	9
Cheirodendron trigynum*	Araliaceae	7
Coprosma rhynchocarpa	Rubiaceae	5
Ilex anomala*	Aquifoliaceae	4
Kokia drynarioides	Malvaceae	8
Metrosideros collina**	Myrtaceae	1, 4, 5, 8, 9
Myrsine lessertiana*	Myrsinaceae	5
Osmanthus sandwicensis	Oleaceae	5
Pelea spp.	Rutaceae	4, 5
Psychotria hawaiiensis var. hillebrandii	Rubiaceae	5
Sophora chrysophylla*	Papilionaceae	7
SHRUBS		
Broussaissia arguta	Saxifragaceae	4
Cassia glauca	Caesalpiniaceae	9
Clermontia parviflora	Campanulaceae	7
Coprosma ernodeoides	Rubiaceae	1, 2, 3
Coprosma montana	Rubiaceae	1
Cyrtandra platyphylla	Gesneriaceae	7
Dodonaea viscosa*	Sapindaceae	1, 2, 6, 8, 9
Fuschsia magellanica var. discolor	Onagraceae	6, 7
Hedyotis centranthoides	Rubiaceae	7
Osteomeles anthyllidifolia	Rosaceae	8, 9
Pipturus hawaiiensis	Urticaceae	4, 5, 7
Rubus hawaiiensis	Rosaceae	1, 4
Rubus penetrans	Rosaceae	5
Rubus rosaefolius	Rosaceae	8
Scaevola chamissoniana	Goodeniaceae	7
Schinus terebinthifolius	Anacardiaceae	9
Solanum pseudocapsicum	Solanaceae	5
Styphelia tameiameiae	Epacridaceae	1, 2, 3, 7, 8
Vaccinium calycinum	Ericaceae	4, 7
Vaccinium reticulatum	Ericaceae	1, 6
Waltheria indica	Sterculiaceae	9
Wikstroemia sandwicensis	Thymelaeaceae	9
VINES		
Alyxia olivaeformis	Apocynaceae	4
Cassytha filiformis	Convolvulaceae	9

TABLE 3. Continued.

SPECIES	FAMILY	PLOT NUMBER(S) (from TABLE 1)
Cocculus ferrandianus	Menispermaceae	8, 9
Ipomoea indica	Convolvulaceae	5
Vitis sp.	Vitaceae	5
FORBS		
Ageratum conyzoides	Compositae	9
Anemone japonica	Ranunculaceae	7
Astelia menziesiana	Liliaceae	4
Bidens pilosa var. minor	Compositae	8
Commelina diffusa	Commelinaceae	5
Eupatorium riparium	Compositae	4, 5, 7
Fragaria vesca var. alba	Rosaceae	5
Hedychium coronarium	Zingiberaceae	6
Hypochaeris radicata	Compositae	1, 2, 3, 4, 6, 7, 8
Nertera granadensis	Rubiaceae	4
Peperomia leptostachya	Piperaceae	4, 9
Peperomia macraeana	Piperaceae	4
Peperomia tetraphylla	Piperaceae	5
Phaius tankervilliae	Orchidaceae	7
Plectranthus australis	Labiatae	9
Rumex acetosella	Polygonaceae	1, 2, 3
Veronica plebeia	Scrophulariaceae	4
Veronica serpyllifolia	Scrophulariaceae	4
GRASSES		
Andropogon glomeratus		6, 8
Andropogon virginicus		6, 8, 9
Dactylis glomerata		5
Deschampsia nubigena		1, 2, 3, 6
Holcus lanatus		1, 2, 3, 5
Isachne distichophylla		7
Rhynchelytrum repens		8
SEDGES		
Carex alligata		4
Carex wahuensis		1, 8
Macharaena angustifolia		6, 7
FERNS		
Asplenium adiantum-nigrum		1, 3
Asplenium trichomanes		1, 3
Cibotium spp.***		4, 7
Microlepia setosa		5

TABLE 3. Concluded.

SPECIES	FAMILY	PLOT NUMBER(S) (from TABLE 1)
Microsorium scolopendria		9
Pellaea ternifolia		1, 3
Pteridium aquilinum		1, 2, 3, 5, 6, 8
Sadleria cyatheoides		6, 7
Sadleria pallida***		4

* = Species also subject to intensive study in other plots (see TABLE 2)

** = Species subject to intensive study by Porter (1972)

*** = Species being studied intensively since June 1972, not reported in this paper in a particular phenophase; in still other cases the phenophase is recorded merely as absent, little, moderate, or heavy for the plant as a whole. When estimates, rather than actual counts, were recorded, observers at first worked in pairs with the author to ensure uniformity in reporting of data.

In order to have numerical data which could be subjected to statistical analyses and presented graphically, it became necessary to establish index values for certain phenophases. For example, in establishing a flowering index, the following values were assigned to each plant:

0 = no flowering

1 = little flowering

2 = moderate flowering

3 = heavy flowering

Then, with a population of 10 plants, the index value for the population will range between 0 and 30. Similar indices have been established for vegetative flush, and for leaf fall.

Conversion of field observations to index values has varied from species to species. For example, flowering in Sophora chrysophylla is recorded as number of inflorescences per tree. Where there are no inflorescences the index value assigned is 0; from 1 to 19 inflorescences the index value assigned is 1; from 20 to 50 inflorescences the index value is 2; with over 50 inflorescences the index value is 3. In other species, where percentage estimates of flowering branches are recorded, an index value of 1 would be assigned when 1% to 5% of the branches were flowering; and index value of 2 when 5% to 25% of the branches were flowering; and an index value of 3 when more then 25% of the branches were flowering. When data have been recorded directly in the field as absent, little, moderate, and heavy, appropriate index values are also assigned directly.

Growth changes in trees are measured by monthly observations on circumference.

Growth values per population within a plot are expressed as average daily change in circumference in microns (μm). These values are obtained by dividing the mean change in circumference since the last observation by the number of days which have elapsed since the last observation and multiplying by 1000 (to convert mm to μm). We have chosen to express our data in terms of circumference rather than in the conventional diameter measurements which most foresters use for these reasons:

a) Circumference is the parameter measured, and no conversion factors need be used.

b) If diameter is measured, errors in reading instruments are 3.14 (π) times as great as when circumference is measured.

c) Trees may not grow equally along all radii in any given period. A circumference measurement, in effect, measures and integrates the changes in all radii, while a diameter measurement measures changes in only two radii.

All statistical treatments of data were made with a Wang 7000 computer, using standard programs supplied with this computer.

RESULTS

Intensive studies

FIGURES 2 to 21 summarize graphically observations made until June 1972 on flowering and vegetative flushing of each population studied intensively. FIGURES 22 to 41 present the changes in circumference of stems in the same populations.

Acacia koa. (FIGS. 3, 5, 7, 11, 19, 23, 25, 27, 31, 39)

Five populations of koa were studied. Flowering in all plots occurred in the winter of 1971-72. At the top of the Mauna Loa Strip Road (FIG. 3) at 6700 feet, flowering began in December, peaked in February and continued through April. At 6000 feet (FIG. 19) the flowering season also started in December, but was of shorter duration, peaking in January and finishing about the end of February. In

FIGS. 2 - 21. Graphs of index values for flowering (————) and for vegetative flushing (- - - - - - -) of each population studied intensively. For the two deciduous species studied, Sapindus saponaria (FIG. 9), and Erythrina sandwicensis (FIG. 13), the leaf fall index values are also graphed (· · · · · · ·).

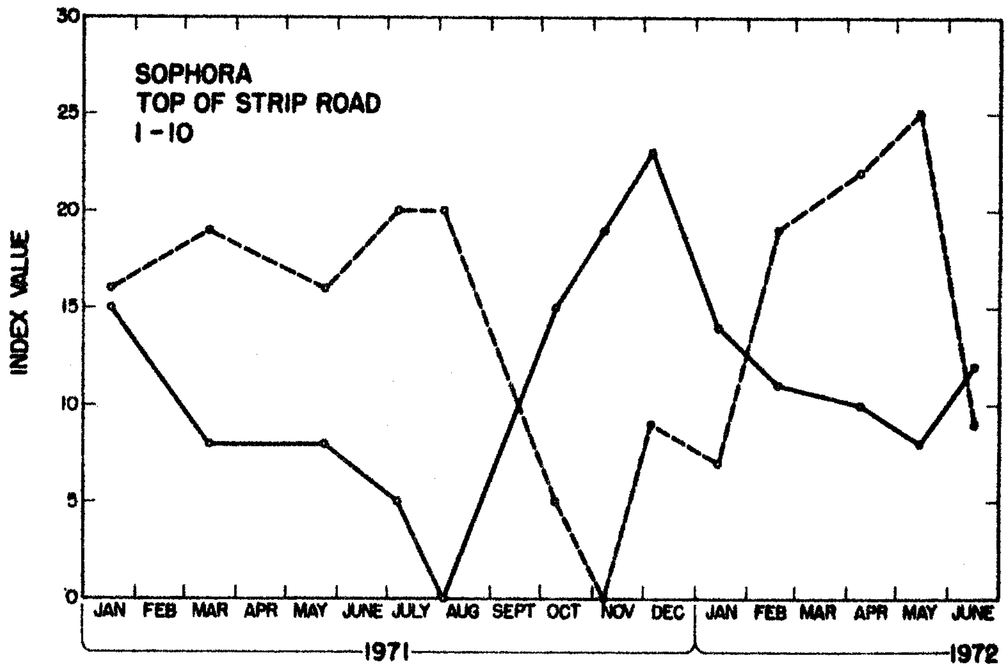

SOPHORA
TOP OF STRIP ROAD
1-10
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 2

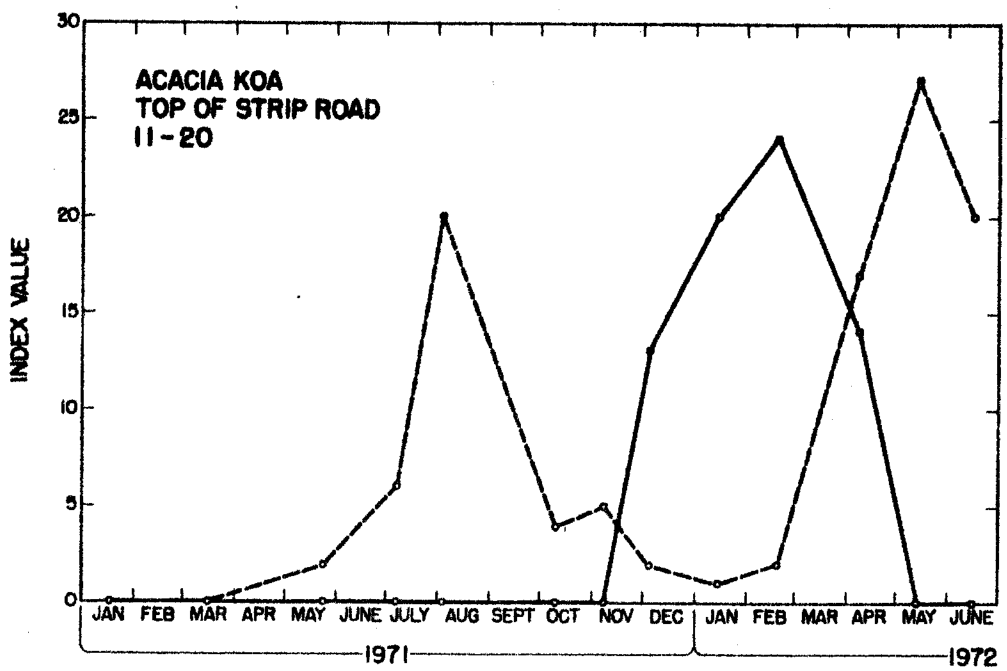

ACACIA KOA
TOP OF STRIP ROAD
11-20
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 3

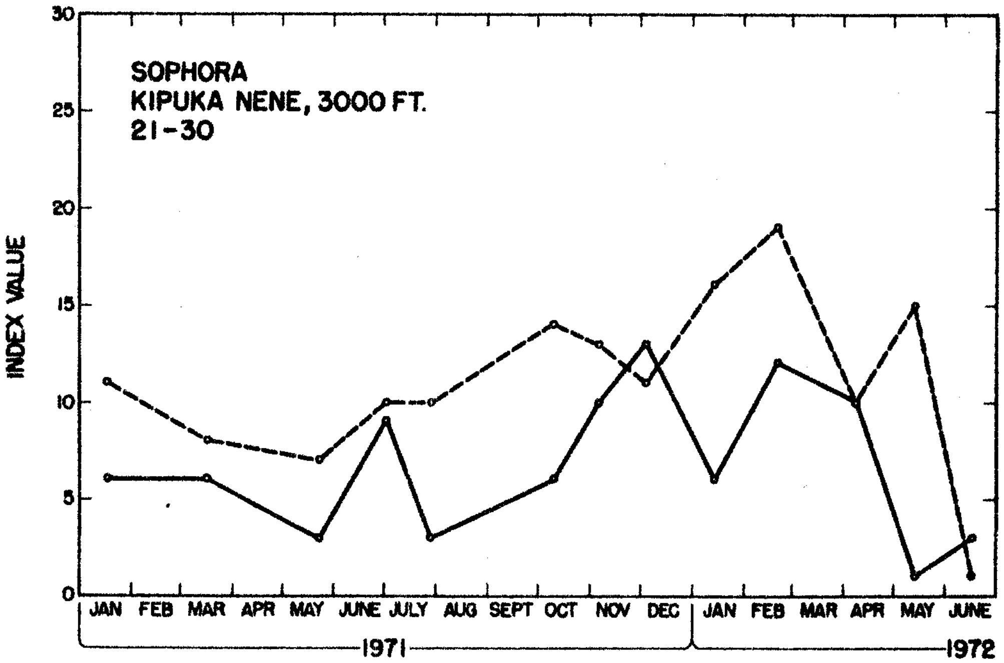

SOPHORA
KIPUKA NENE, 3000 FT.
21-30
INDEX VALUE
0
5
10
15
20
25
30
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 4

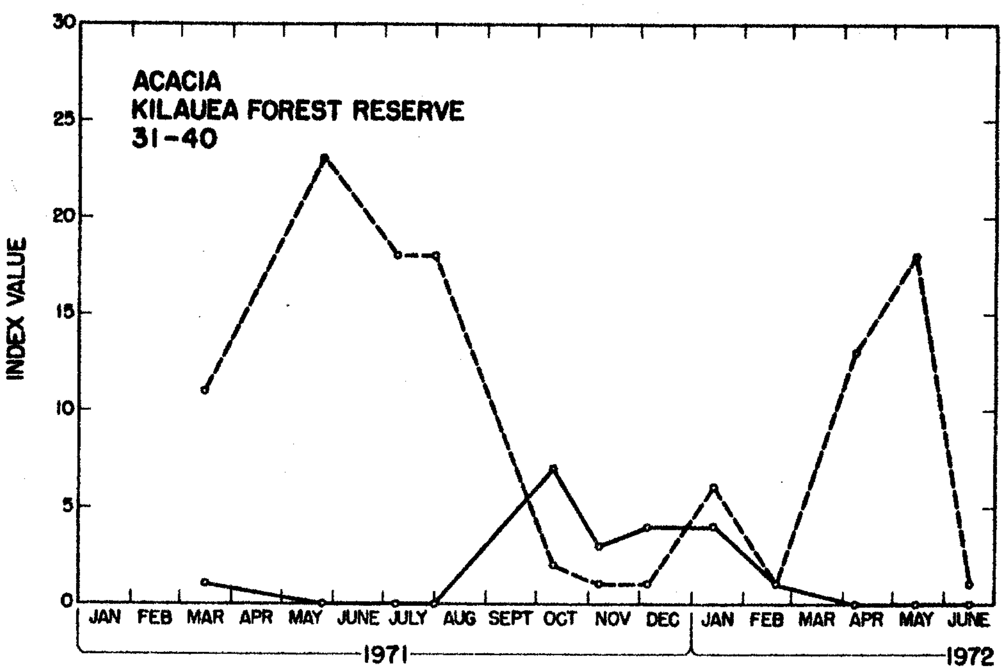

ACACIA
KILAUEA FOREST RESERVE
31-40
INDEX VALUE
0
5
10
15
20
25
30
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 5

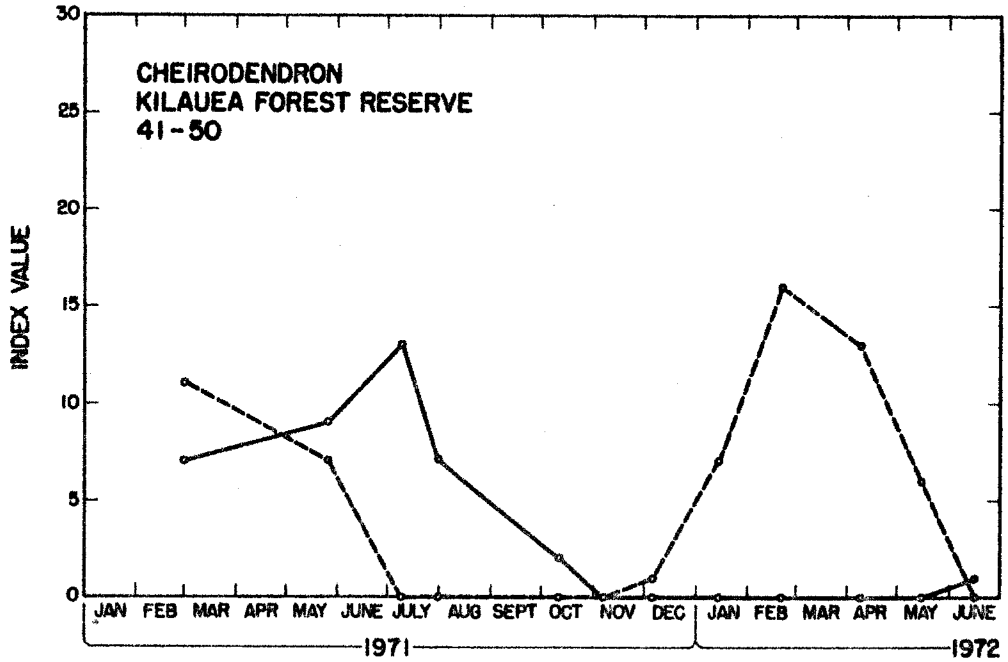

CHEIRODENDRON
KILAUEA FOREST RESERVE
41-50
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 6

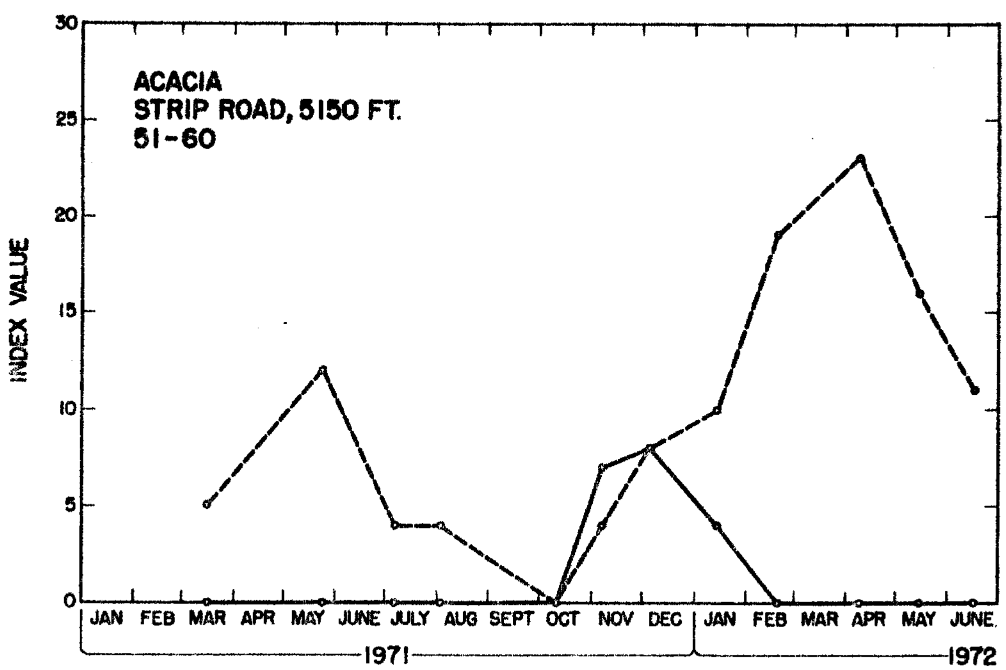

ACACIA
STRIP ROAD, 5150 FT.
51-60
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 7

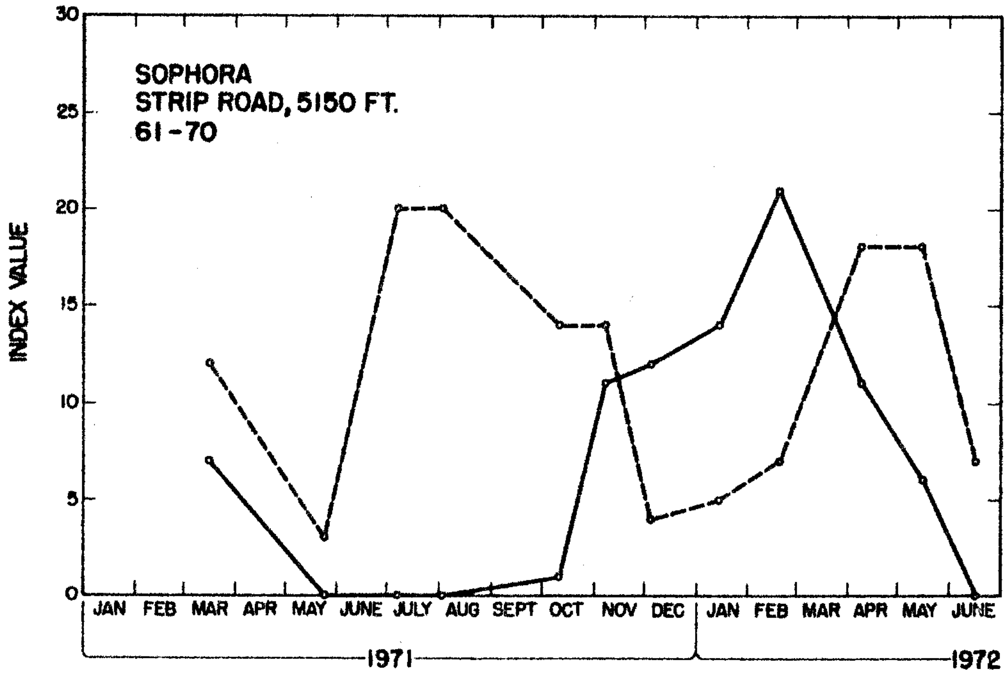

SOPHORA
STRIP ROAD, 5150 FT.
61-70
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 8

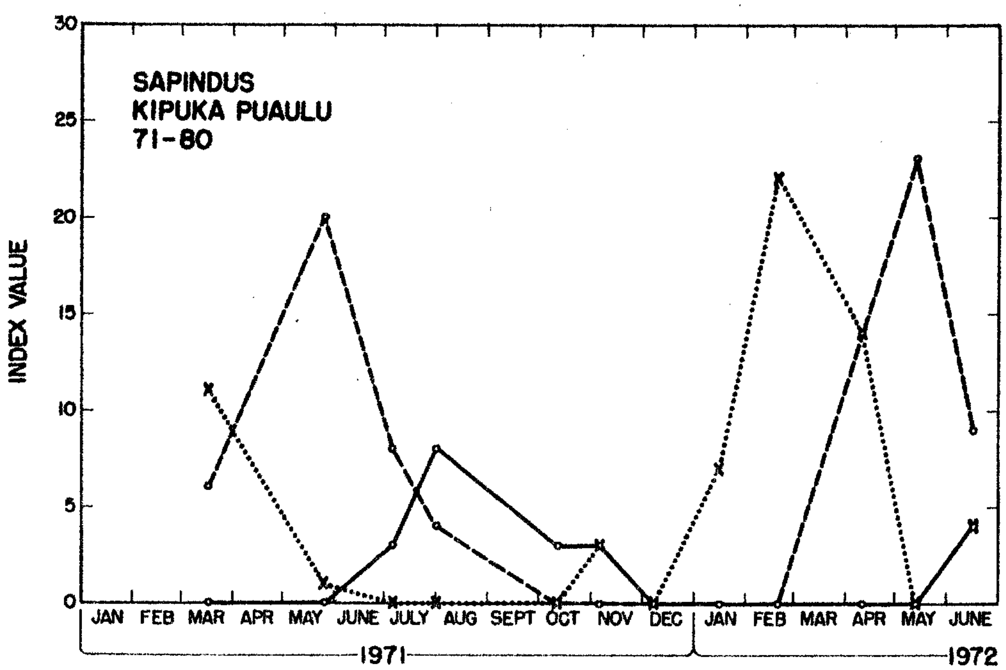

SAPINDUS
KIPUKA PUAULU
71-80
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 9

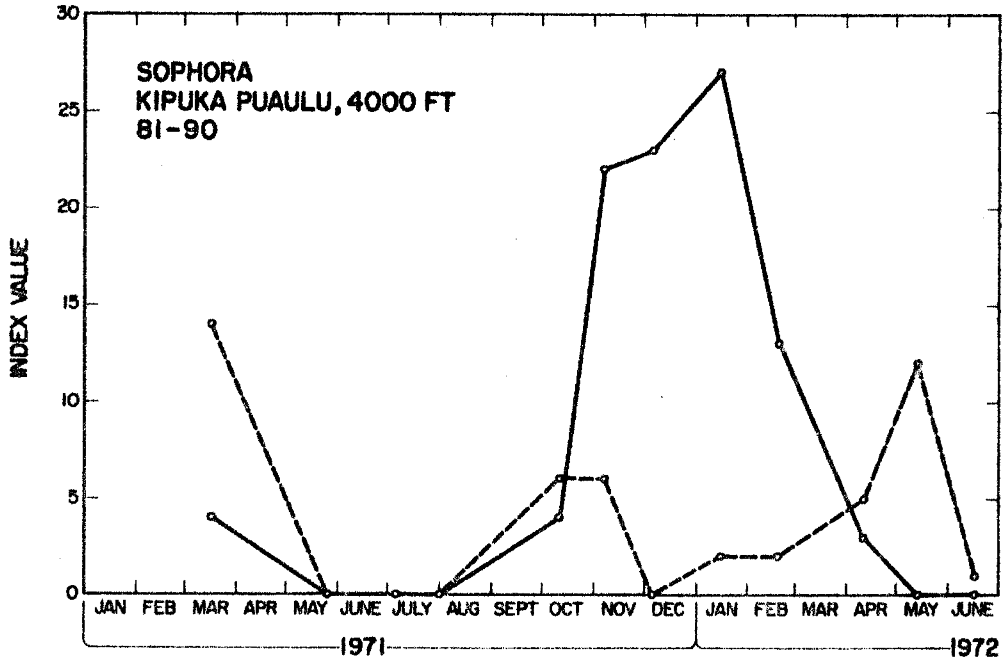

SOPHORA
KIPUKA PUAULU, 4000 FT
81-90
INDEX VALUE
0
5
10
15
20
25
30
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 10

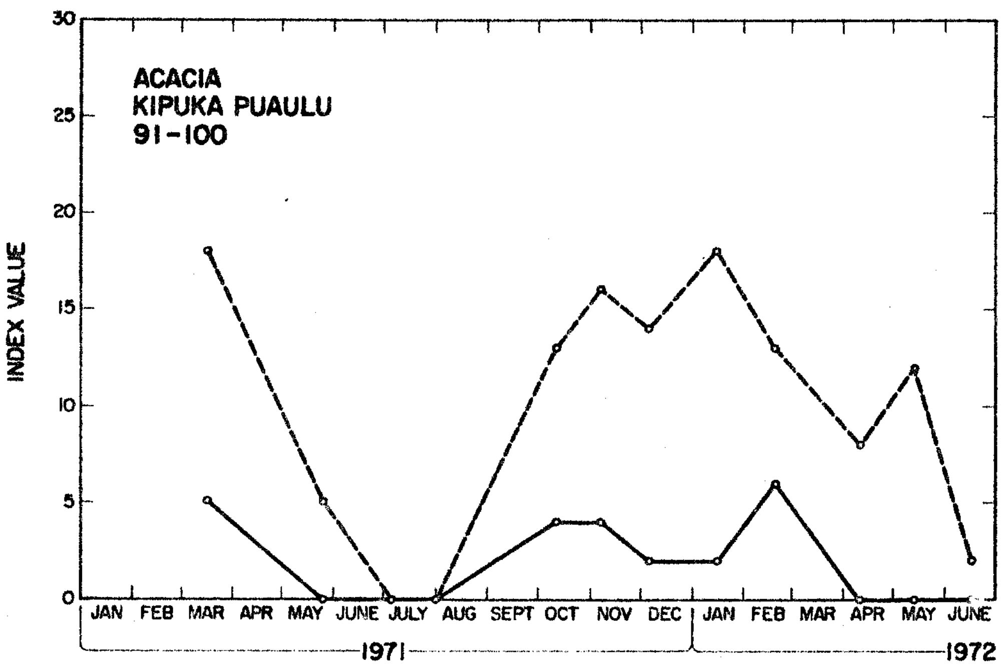

ACACIA
KIPUKA PUAULU
91-100
INDEX VALUE
0
5
10
15
20
25
30
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 11

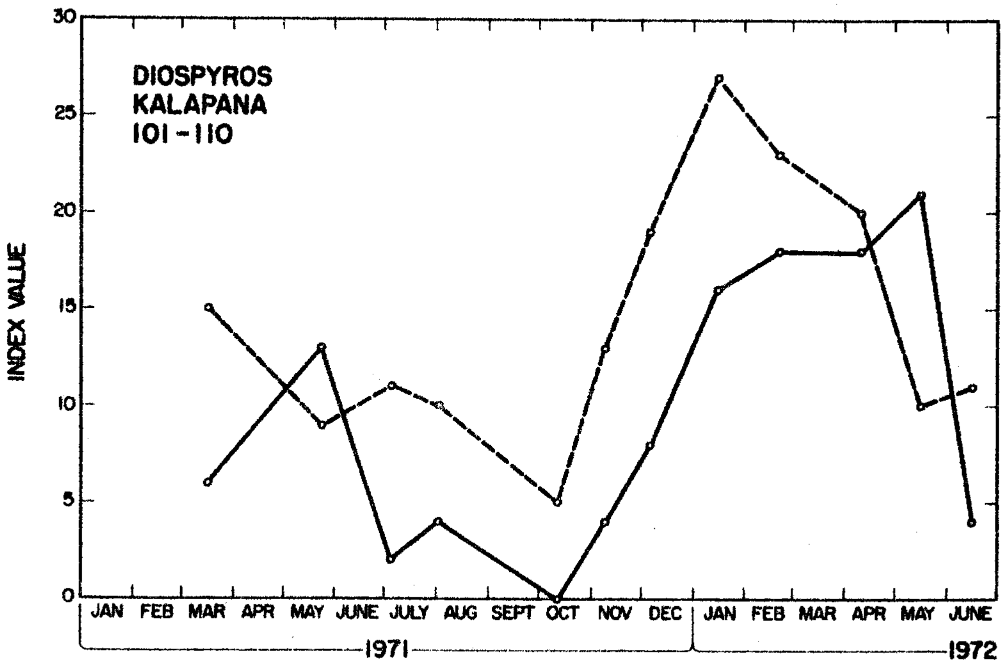

DIOSPYROS
KALAPANA
101 - 110
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 12

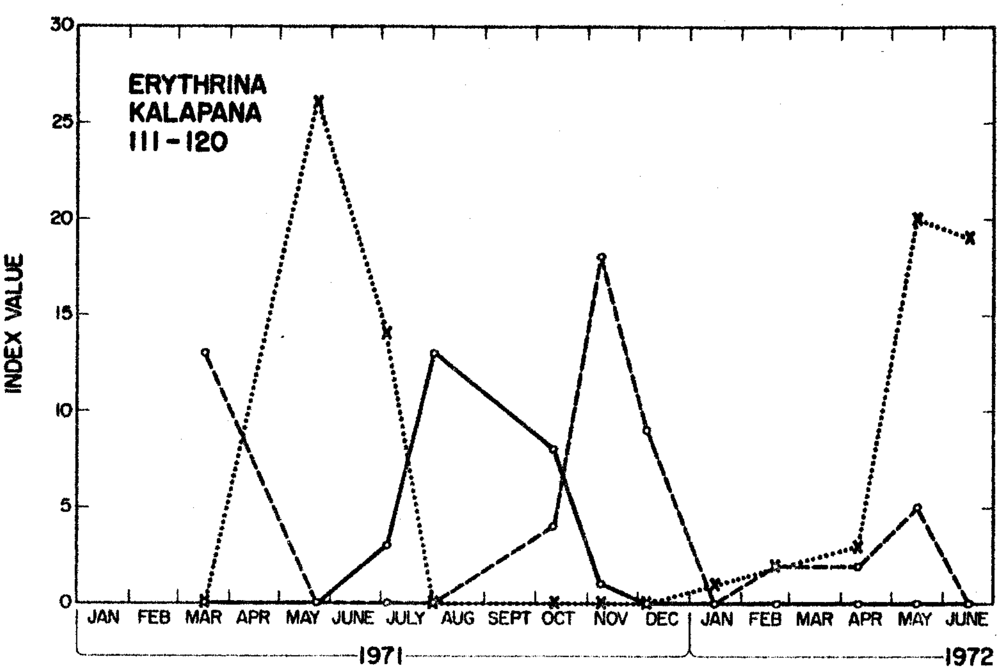

ERYTHRINA
KALAPANA
111 - 120
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 13

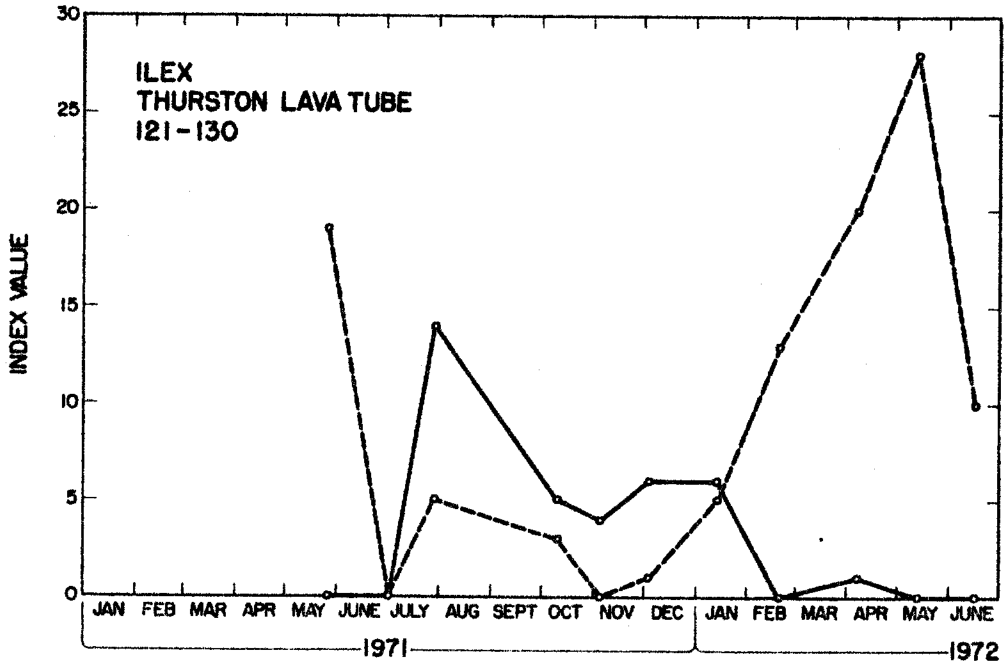

ILEX
THURSTON LAVA TUBE
121-130
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 14

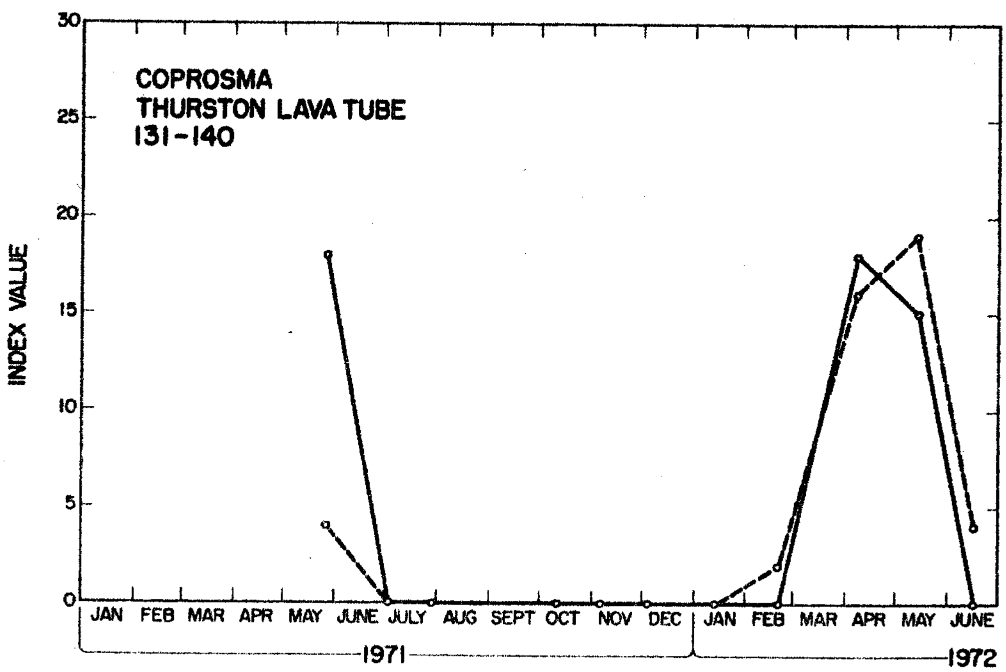

COPROSMA
THURSTON LAVA TUBE
131-140
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 15

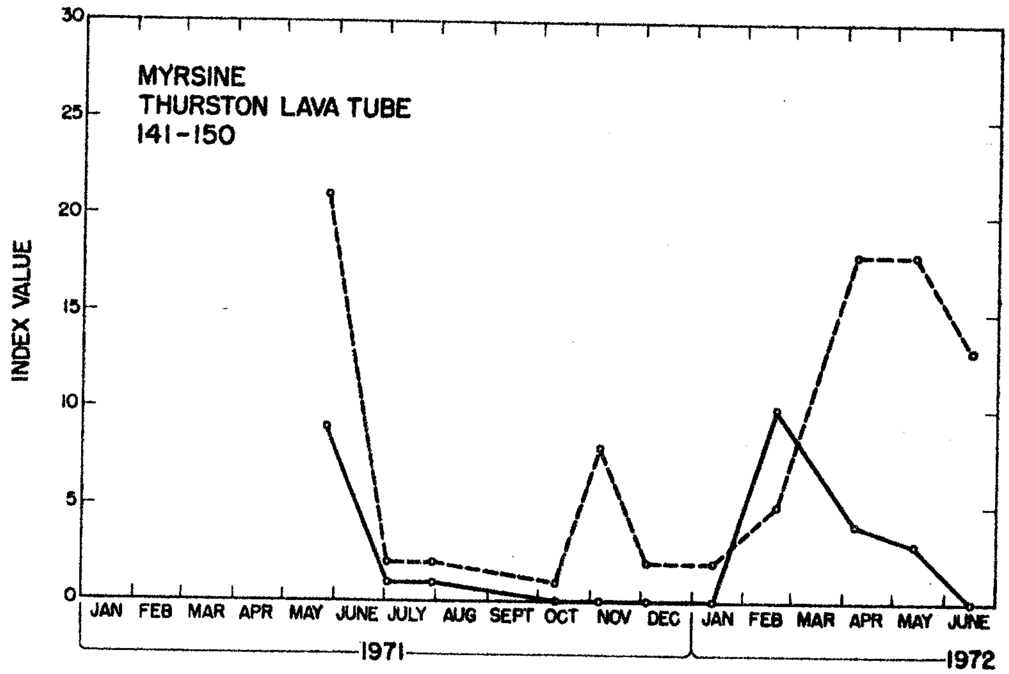

MYRSINE
THURSTON LAVA TUBE
141-150
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 16

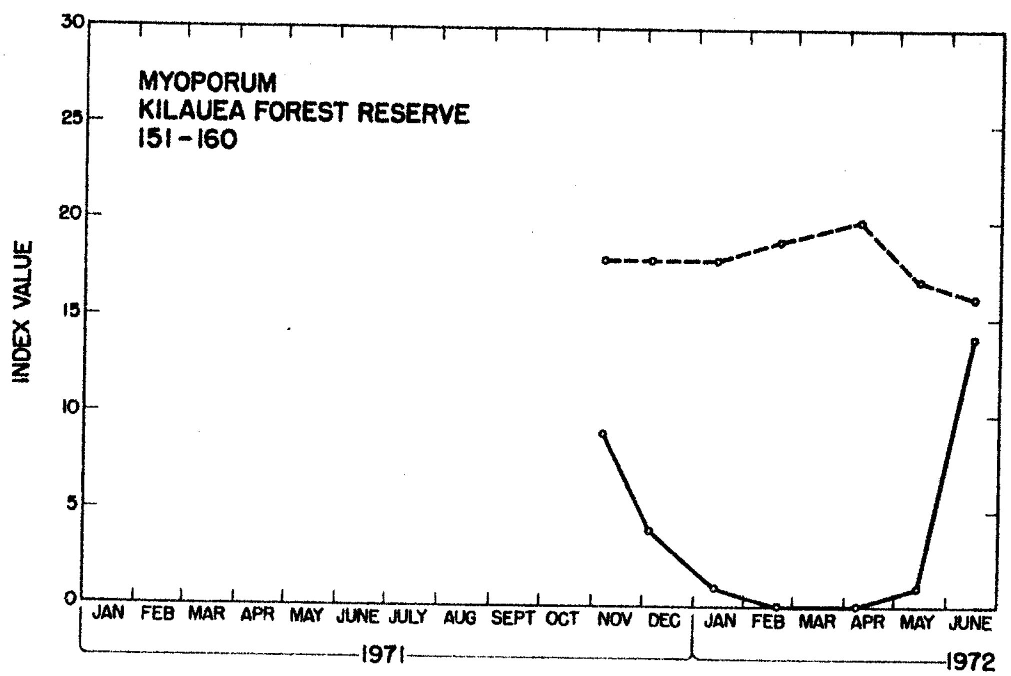

MYOPORUM
KILAUEA FOREST RESERVE
151-160
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 17

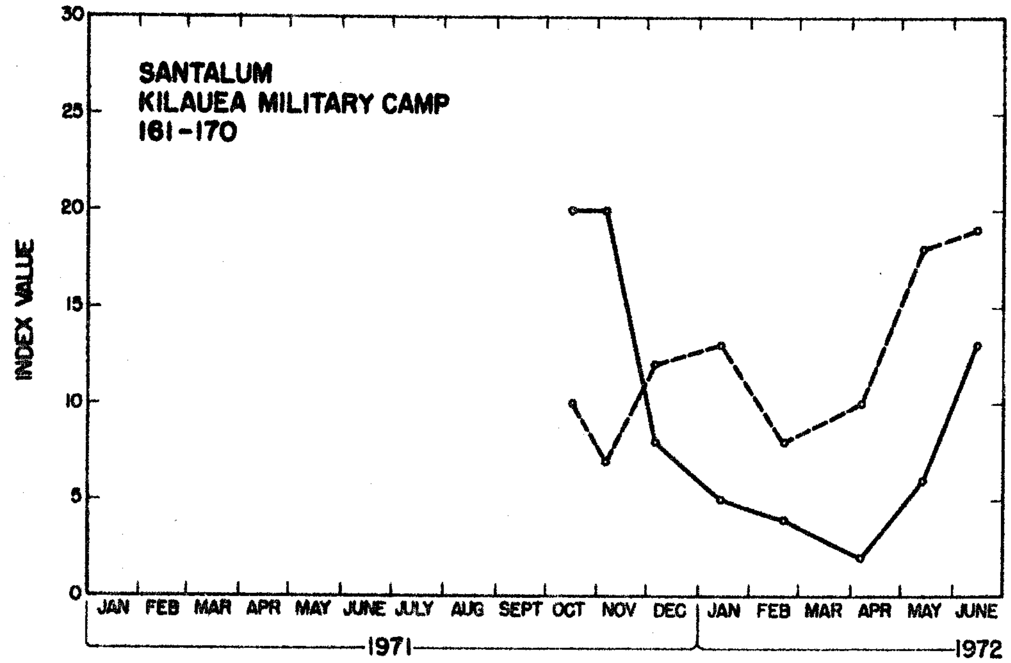

SANTALUM
KILAUEA MILITARY CAMP
161-170
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 18

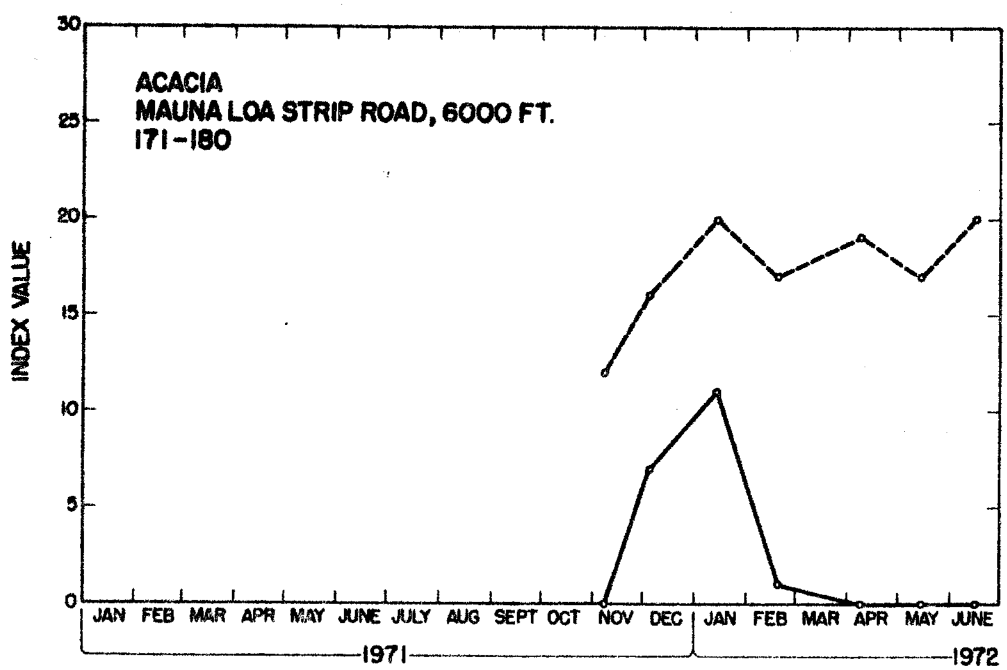

ACACIA
MAUNA LOA STRIP ROAD, 6000 FT.
171-180
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 19

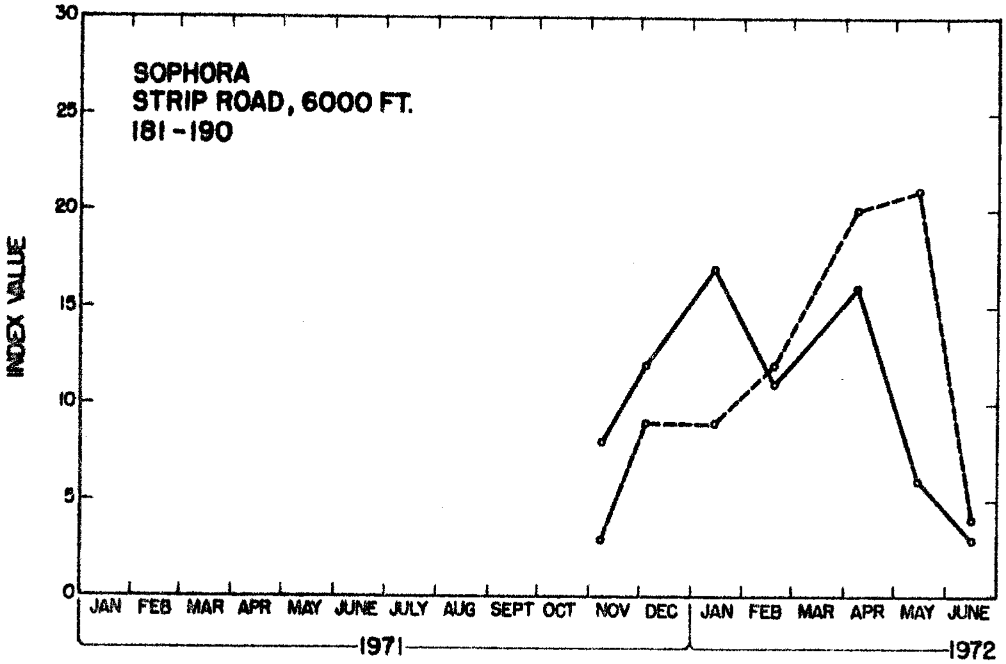

SOPHORA
STRIP ROAD, 6000 FT.
181-190
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 20

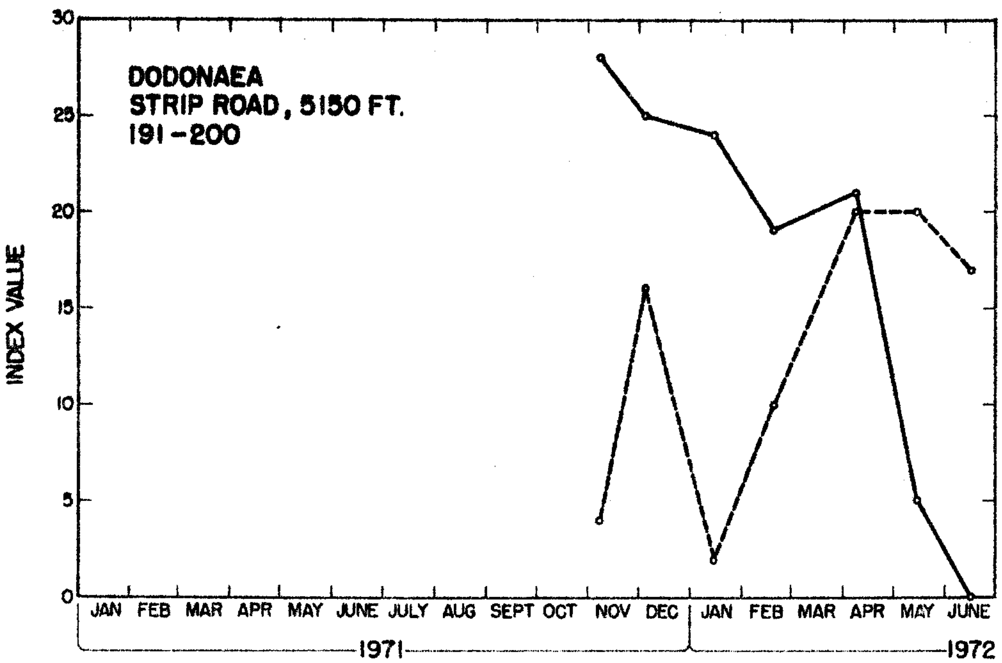

DODONAEA
STRIP ROAD, 5150 FT.
191-200
INDEX VALUE
30
25
20
15
10
5
0
JAN FEB MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
1971
1972

FIG. 21

FIGS. 22 - 41. Graphs of average daily changes in stem circumference of each population studied intensively. Positive values indicate increases in stem circumference during the periods indicated, while negative values indicate shrinkage. The horizontal dashed lines in FIGS. 22 - 36 indicate the average daily change in circumference during the first year of the study. Populations shown in FIGS. 37 - 41 have been studied less than one year, hence no annual average is shown.

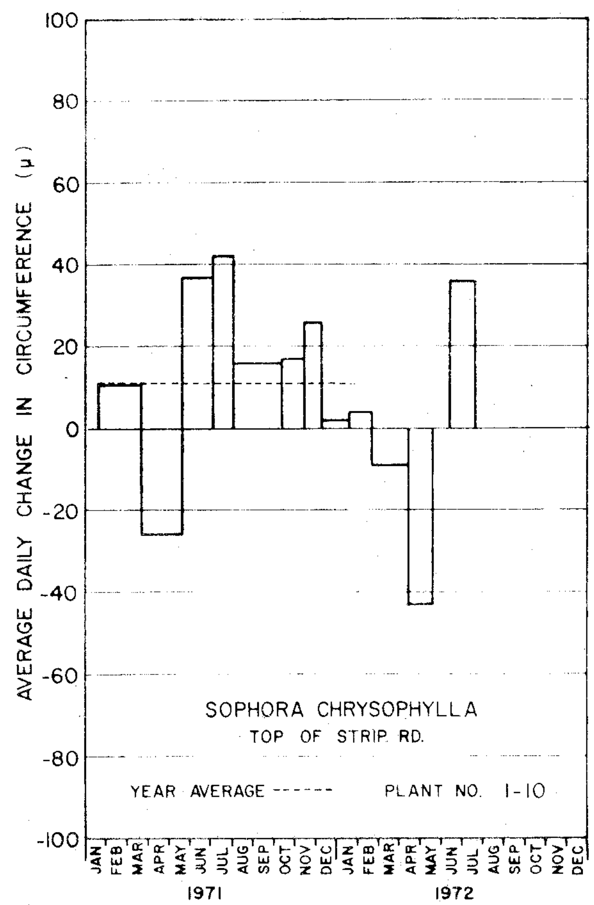

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (µ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
SOPHORA CHRYSOPHYLLA
TOP OF STRIP RD.
YEAR AVERAGE ------
PLANT NO. 1-10
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 22

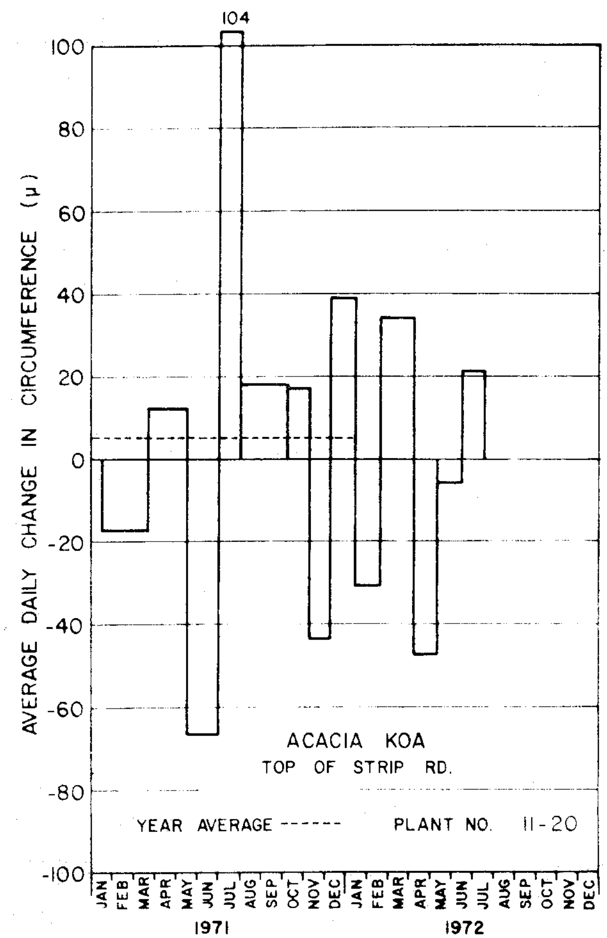

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (µ)
104
100
80
60
40
20
0
-20
-40
-60
-80
-100
ACACIA KOA
TOP OF STRIP RD.
YEAR AVERAGE ------
PLANT NO. 11-20
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 23

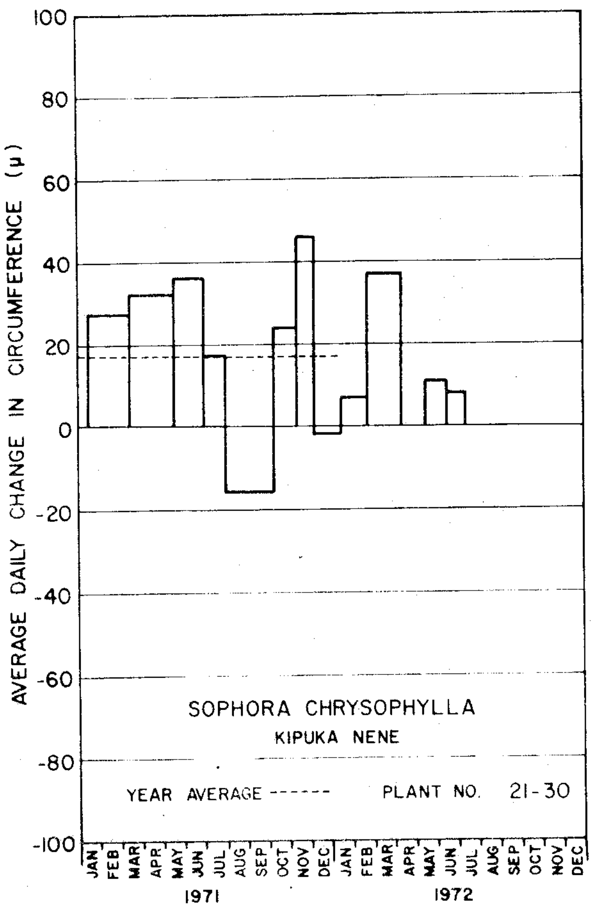

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
SOPHORA CHRYSOPHYLLA
KIPUKA NENE
YEAR AVERAGE ------
PLANT NO. 21-30
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 24

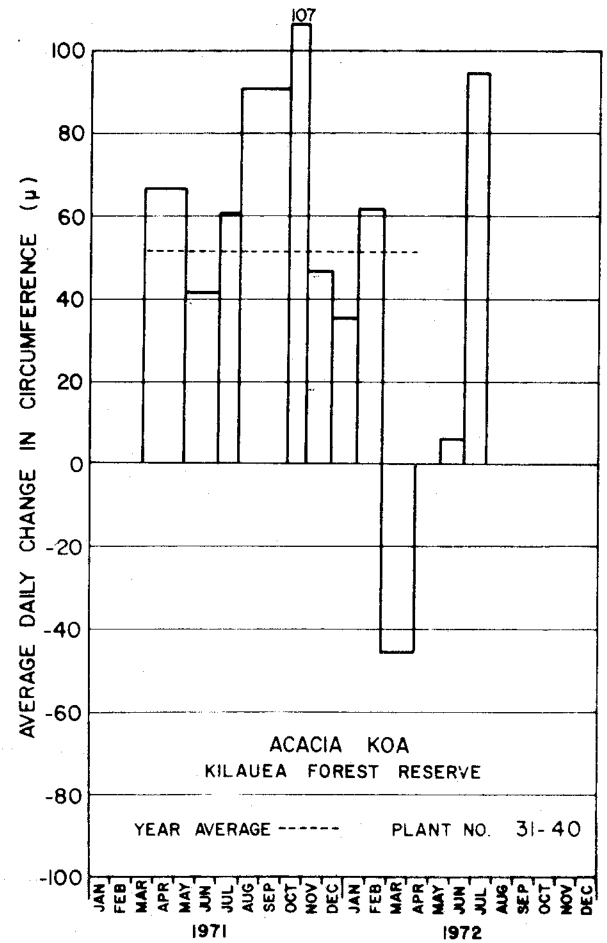

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
107
100
80
60
40
20
0
-20
-40
-60
-80
-100
ACACIA KOA
KILAUEA FOREST RESERVE
YEAR AVERAGE ------
PLANT NO. 31-40
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 25

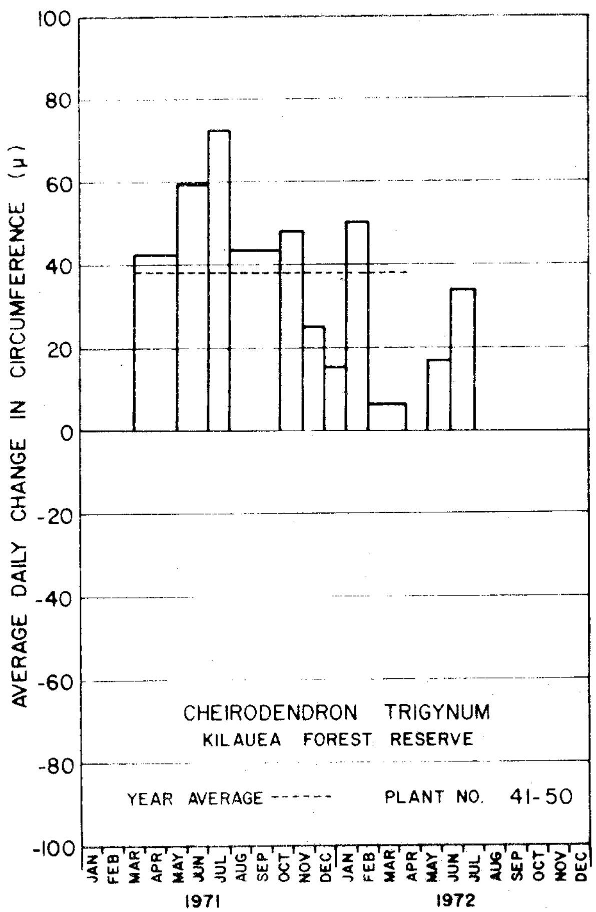

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
CHEIRODENDRON TRIGYNUM
KILAUEA FOREST RESERVE
YEAR AVERAGE ------
PLANT NO. 41-50
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 26

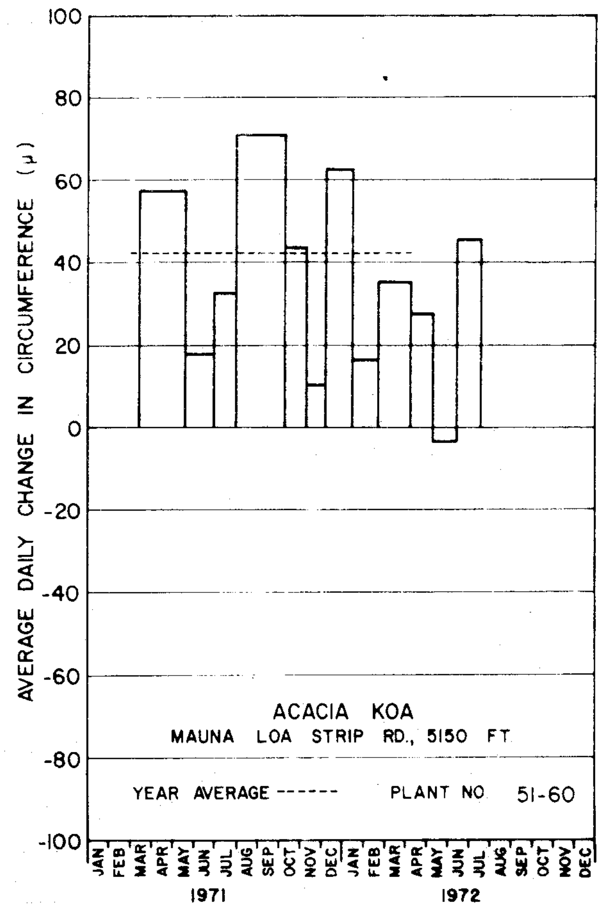

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
ACACIA KOA
MAUNA LOA STRIP RD., 5150 FT
YEAR AVERAGE ------
PLANT NO 51-60
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 27

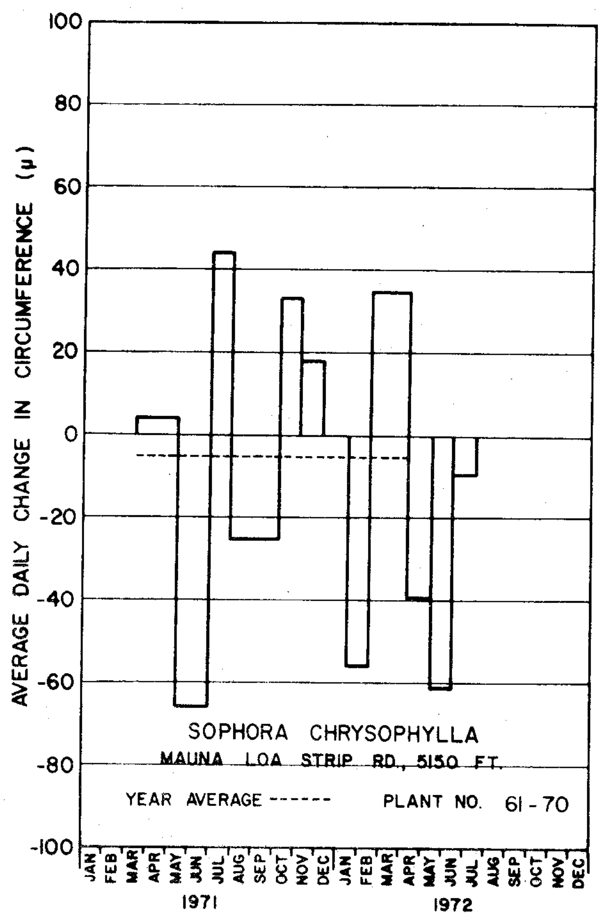

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
SOPHORA CHRYSOPHYLLA
MAUNA LOA STRIP RD., 5150 FT.
YEAR AVERAGE ------
PLANT NO. 61-70
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 28

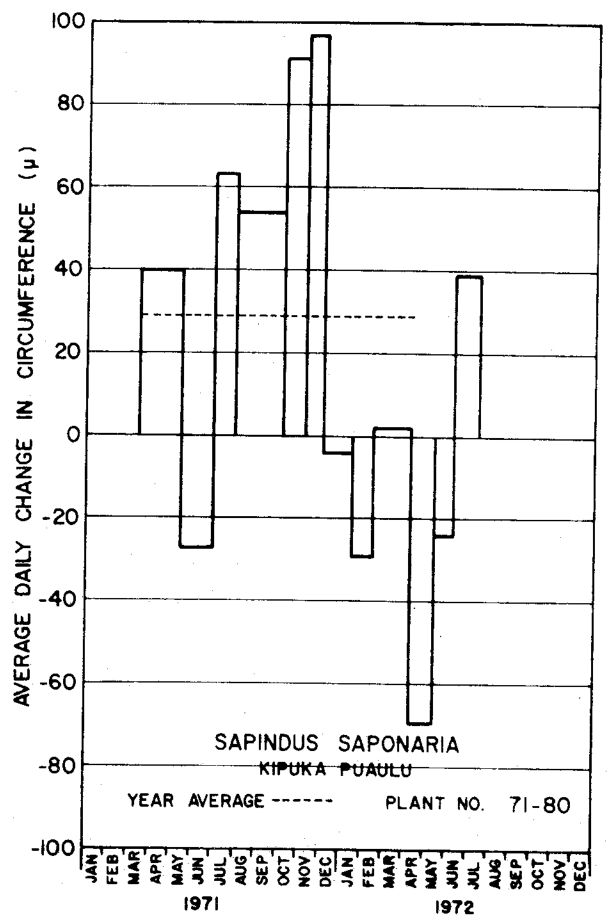

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
SAPINDUS SAPONARIA
KIPUKA PUAULU
YEAR AVERAGE ------
PLANT NO. 71-80
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 29

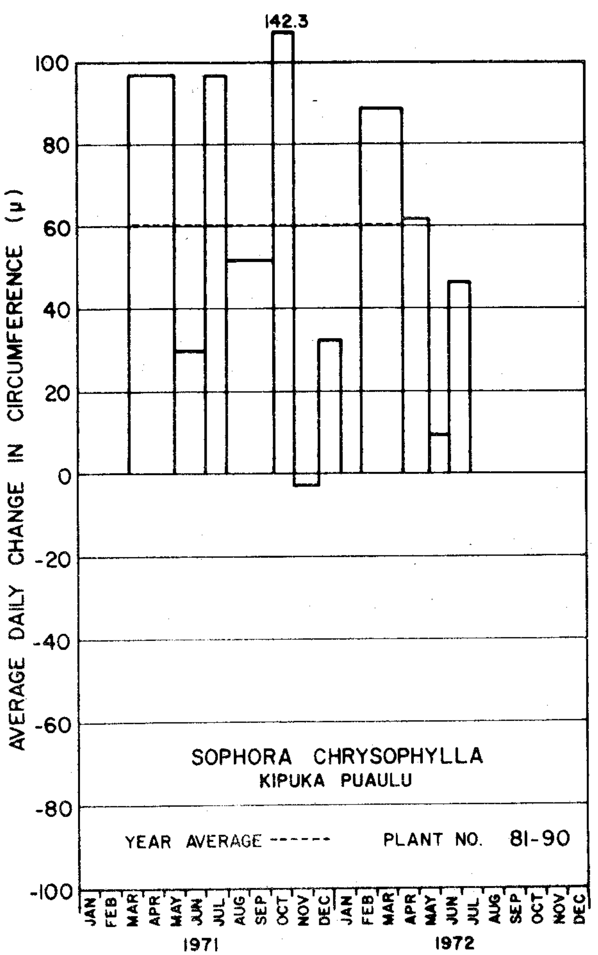

142.3
AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
SOPHORA CHRYSOPHYLLA
KIPUKA PUAULU
YEAR AVERAGE ------
PLANT NO. 81-90
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 30

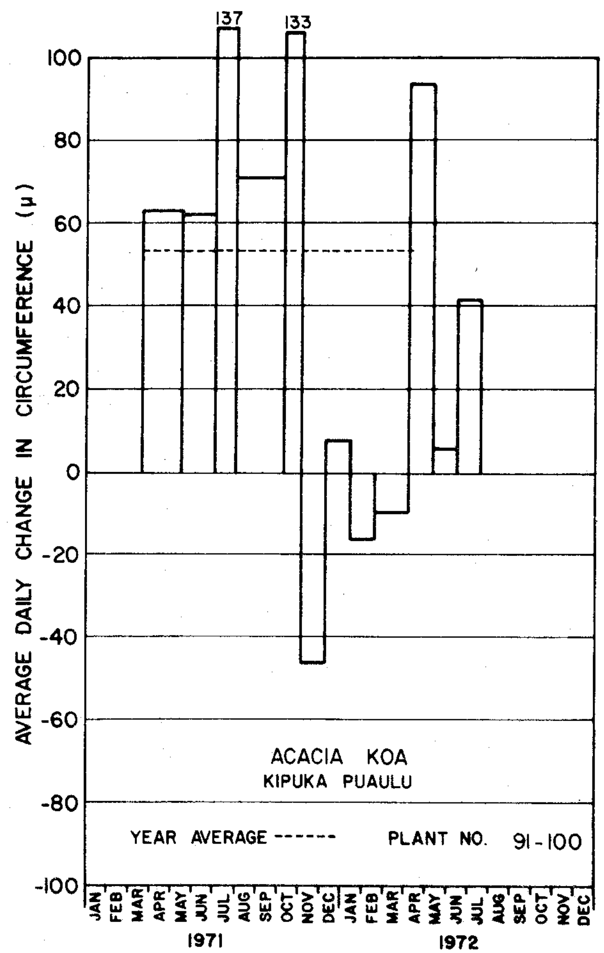

137
133
AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
ACACIA KOA
KIPUKA PUAULU
YEAR AVERAGE ------
PLANT NO. 91-100
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 31

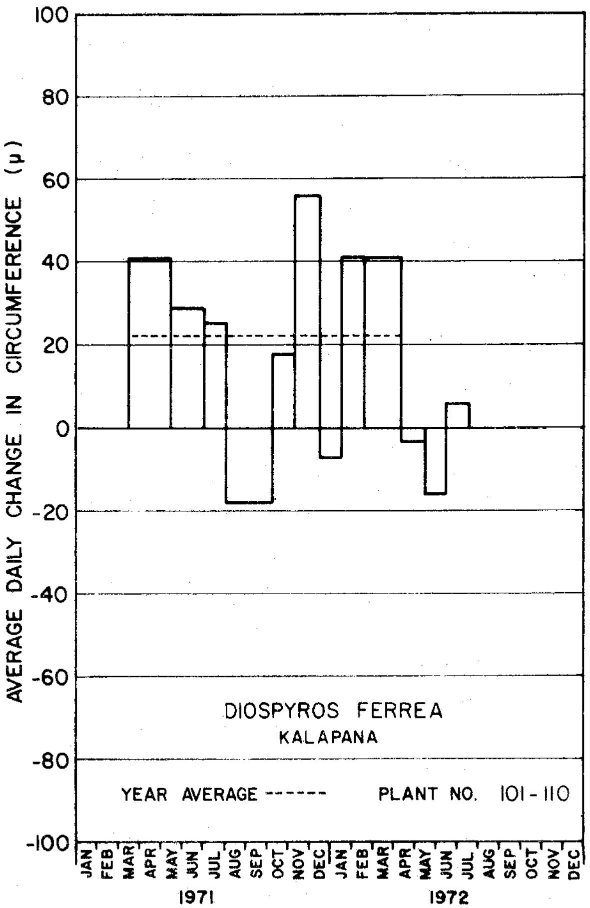

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
DIOSPYROS FERREA
KALAPANA
YEAR AVERAGE ------
PLANT NO. 101-110
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 32

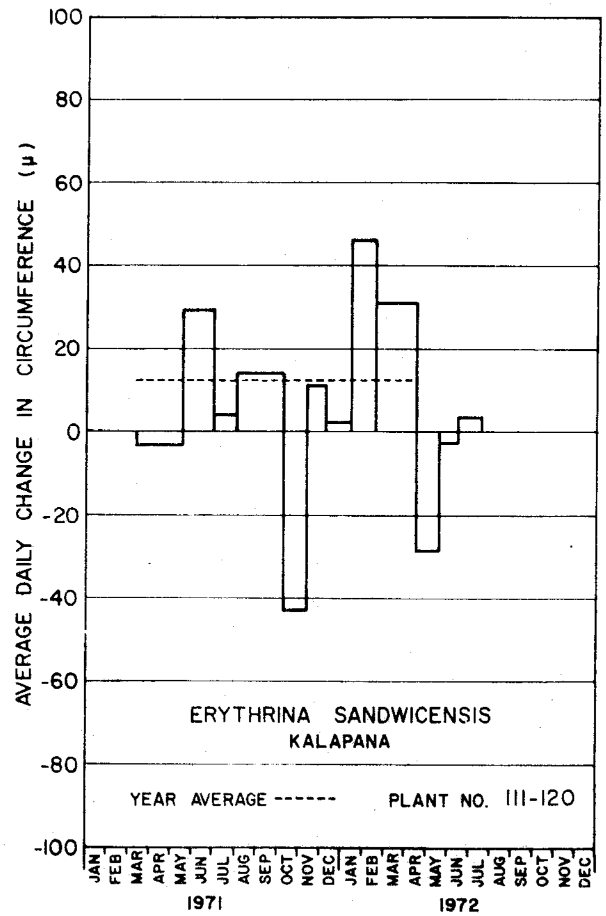

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
ERYTHRINA SANDWICENSIS
KALAPANA
YEAR AVERAGE ------
PLANT NO. 111-120
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 33

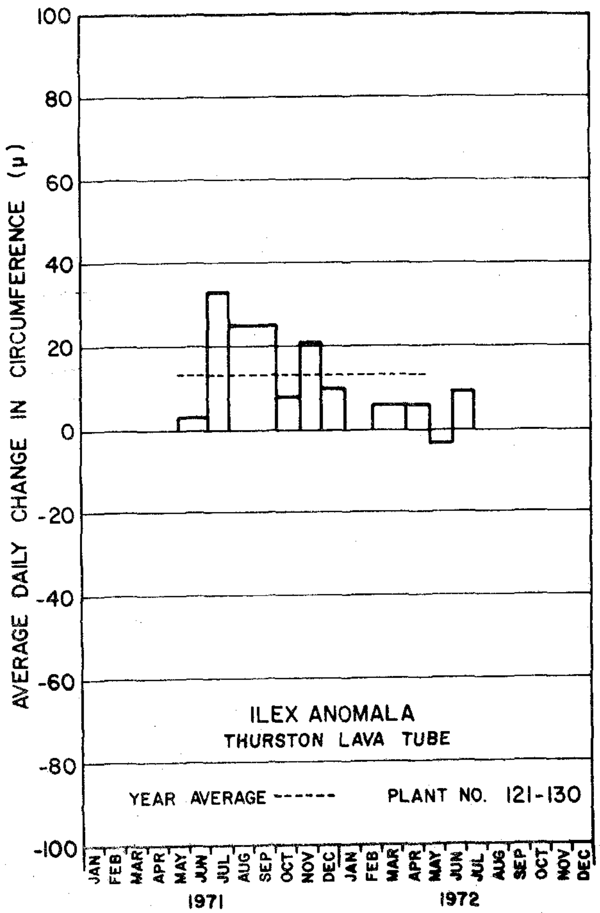

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
ILEX ANOMALA
THURSTON LAVA TUBE
YEAR AVERAGE ------
PLANT NO. 121-130
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 34

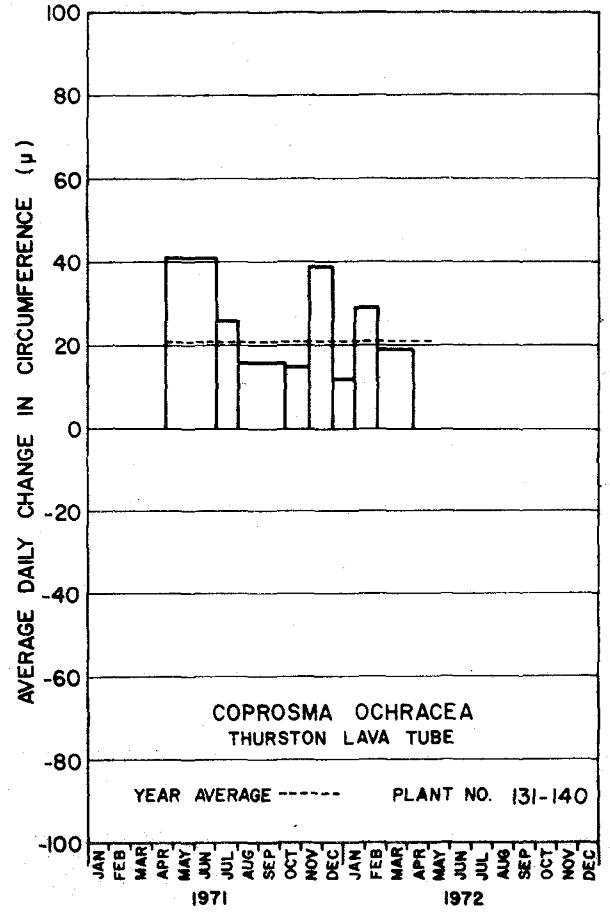

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
COPROSMA OCHRACEA
THURSTON LAVA TUBE
YEAR AVERAGE ------
PLANT NO. 131-140
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 35

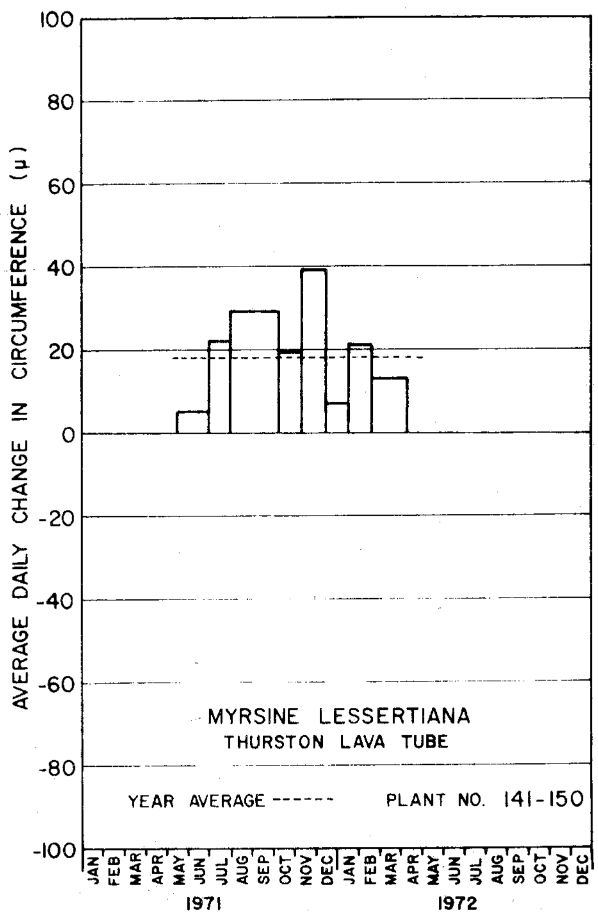

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
MYRSINE LESSERTIANA
THURSTON LAVA TUBE
YEAR AVERAGE ------
PLANT NO. 141-150
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 36

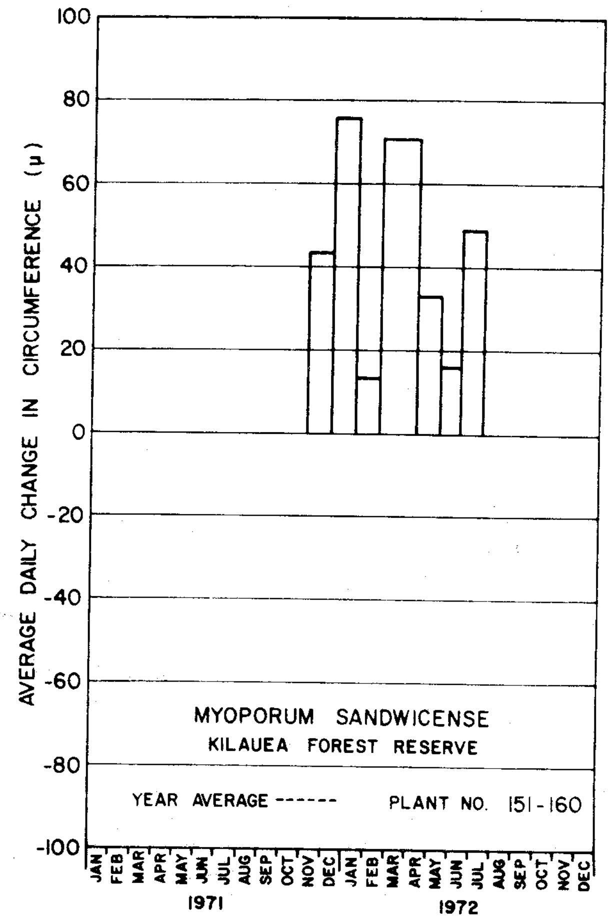

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
MYOPORUM SANDWICENSE
KILAUEA FOREST RESERVE
YEAR AVERAGE ------
PLANT NO. 151-160
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 37

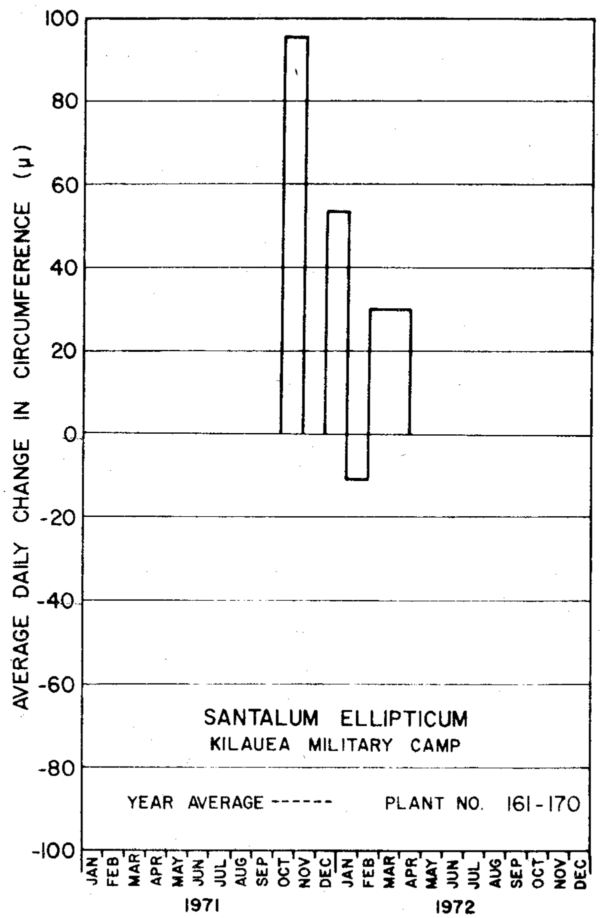

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
SANTALUM ELLIPTICUM
KILAUEA MILITARY CAMP
YEAR AVERAGE ------
PLANT NO. 161-170
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 38

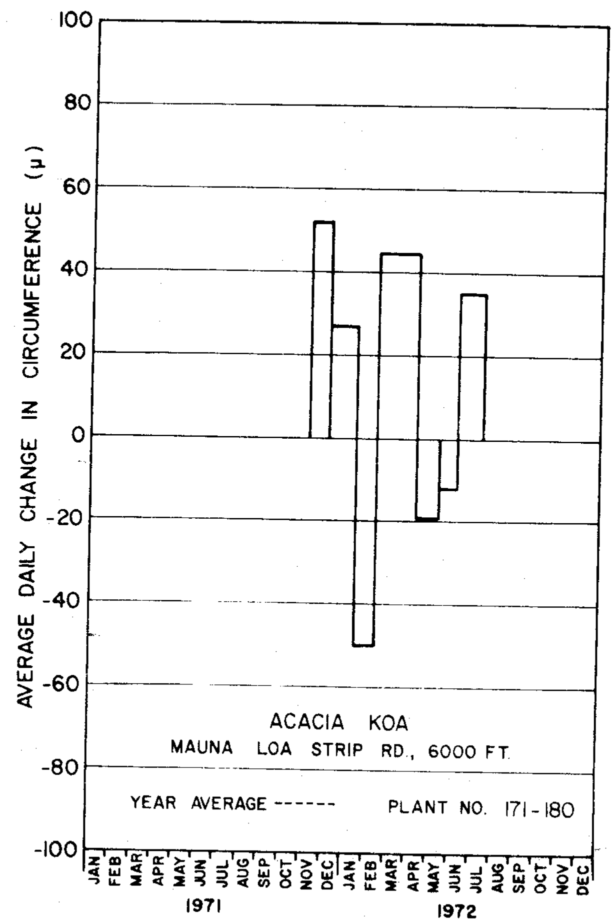

AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
ACACIA KOA
MAUNA LOA STRIP RD., 6000 FT.
YEAR AVERAGE ------
PLANT NO. 171-180
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 39

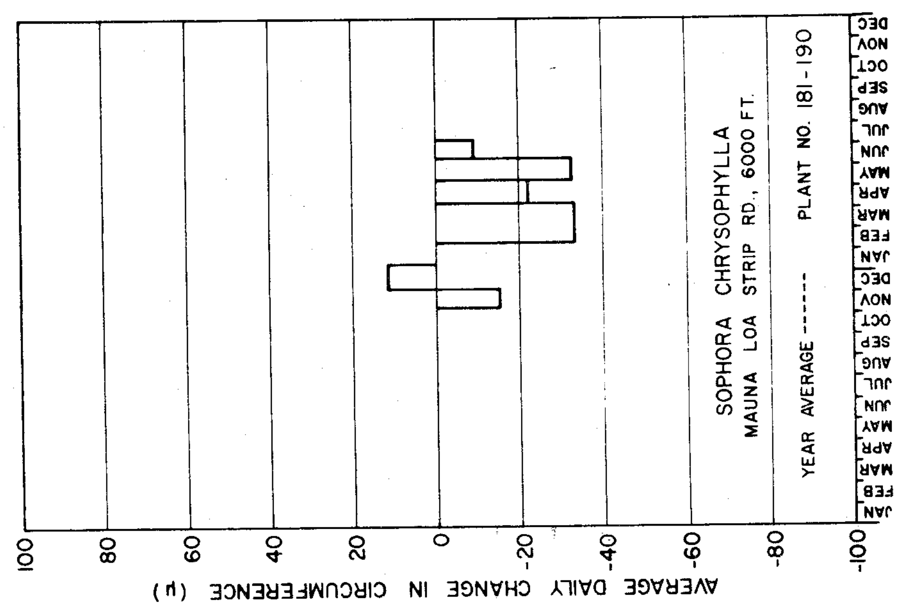

SOPHORA CHRYSOPHYLLA
MAUNA LOA STRIP RD., 6000 FT.
YEAR AVERAGE ------
PLANT NO. 181-190
AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 40

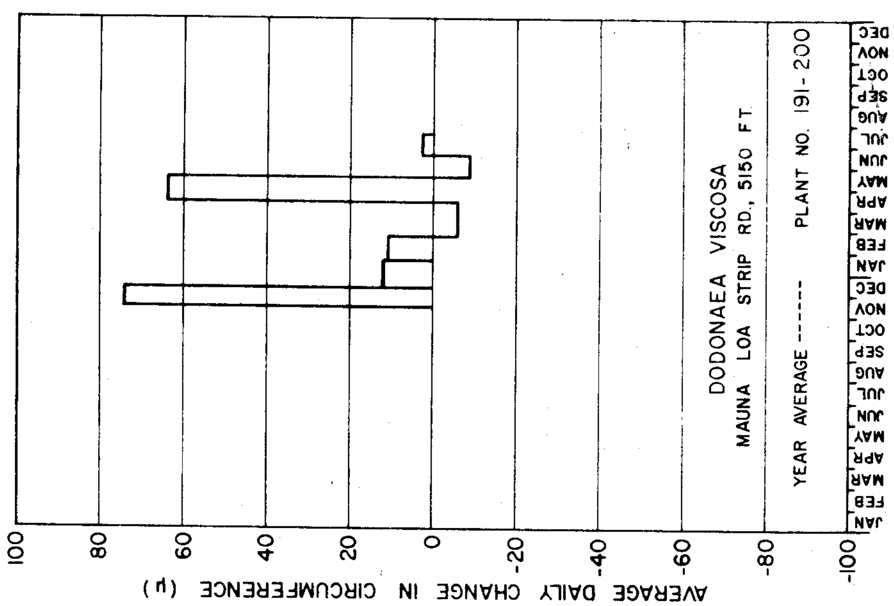

DODONAEA VISCOSA
MAUNA LOA STRIP RD., 5150 FT.
YEAR AVERAGE ------
PLANT NO. 191-200
AVERAGE DAILY CHANGE IN CIRCUMFERENCE (μ)
100
80
60
40
20
0
-20
-40
-60
-80
-100
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
1972

FIG. 41

the Kilauea Forest Reserve (FIG. 5) at 5400 feet flowering was at its peak in October (it probably started in early September, but no observations were made that month) and continued through February. At 5150 feet on the Strip Road (FIG. 7) flowering started in late October, peaked in December, and was finished by early February. At 4000 feet in Kipuka Puaulu (FIG. 11), flowering was well underway in October, (probably starting in September), and continued through the end of March.

All plots except the one at 6000 feet were observed from early in 1971. No flowering was evident during the winter of 1970-71 in the plots at 6700 feet and 5150 feet. A few trees were flowering in March 1971 at 4000 feet, and one tree had a few flowers in March 1971 in the Kilauea Forest Reserve. These data indicate that very little flowering of koa occurred in the winter of 1971-72. Even so, only the plot at the top of the Strip Road had a majority of the trees with moderate to large numbers of flowers at any one time. In the other plots, with only one exception (January 1972 in the 6000 foot plot), flowering index values were less than 10 at each date of observation. Thus, even in a year of heavier flowering, the amount of flowering in koa seems to be quite low.

The time of peak vegetative flushing of koa differed from plot to plot. At the top of the Strip Road flushing occurred in the summer in both 1971 and 1972, and very little flushing occurred during the winter. In this population (FIG. 3) there was a clear alternation between peak flushing, peak flowering, and peak flushing again. At 6000 feet on the Strip Road flushing has been constantly high from November 1971 through June 1972, and does not seem to have decreased during the peak flowering period (FIG. 19). The pattern in the Kilauea Forest Reserve (FIG. 5) resembles that at the top of the Strip Road - peak flushes in summer months, dropping off during the spring (March through May) in both years, but considerable flushing also occurred from November 1971 through January 1972 which was the time of peak flowering. In Kipuka Puaulu at 4000 feet, peak flushing occurred during fall, winter, and spring, and dropped off during the summer. Peak flowering thus occurred at the same time as peak flushing (FIG. 11).

In a general way we can summarize our observations on flowering and flushing in koa thus:

During 1970-71 very little flowering occurred. In 1971-72 peak flowering occurred during the winter months. At higher elevations peak flushing occurred during the summer and periods of peak flushing and peak flowering seem to alternate. At lower elevations periods of peak flowering and peak flushing tend to coincide.

As Lanner observed (1965), very few fruits developed to maturity on koa trees in this area. We have not yet observed enough to be able to make any statements about the seasonality of fruit development or seed drop.

Circumference changes in koa varied from plot to plot. While all cambial samples taken indicated that the vascular cambium was active at the time of sampling, annual growth was much higher in the three lower-elevation plots, Kipuka Puaulu, Kilauea Forest, and 5150 feet on the Strip Road. At 5150 feet, while growth varied greatly from month to month (FIG. 27), all months but one showed a positive value, and no pronounced seasonal variation is evident. At Kipuka Puaulu (FIG. 31) and Kilauea Forest (FIG. 25) growth rates tended to be higher in the summer months and lower or even negative during the winter. In the plots at 6000 feet (FIG. 39) and 6700 feet (FIG. 23), the figures fluctuate so widely from month to month that no seasonal correlations are evident. It should be noted, however, that the plot at 6700 feet is located near the upper edge of the range of koa on the south slope of Mauna Loa.

Sophora chrysophylla. (FIGS. 2, 4, 8, 10, 20, 22, 24, 28, 30, 40)

The flowering pattern in mamane is, at this point, still confusing to interpret. At the top of the Strip Road at 6700 feet (FIG. 2) there is a definite flowering peak in the late fall months. In the summer of 1971 flowering dropped to zero but in the summer of 1972 there was still considerable flowering in June (and some in July, although it does not show on the graph). At 6000 feet (FIG. 20) the winter months seem to be the time of peak flowering, as is the case at 5150 feet (FIG. 8). The 5150 feet plot has been observed for 18 months and during the summers of both years flowering dropped to zero. Again at 4000 feet (FIG. 10) winter is the peak flowering season. At 3000 feet (FIG. 4) however, flowering occurs throughout the year. Flowering was very low in the summer of 1972, but was much higher in the summer of 1971.

Flowering patterns at 3000, 4000, and 5150 feet are similar to those described by Baldwin (1953) from the same areas.

The seasonality of vegetative flushing in Sophora is also puzzling. At 6700 feet (FIG. 2) the amount of flushing appears to be inversely related to the amount of flowering, with flushing lower in late fall when flowering is heaviest, and heaviest in the spring and early summer when flowering is lightest. The data we have obtained from 8 months of observations at 6000 feet (FIG. 20) suggest that a similar relationship may occur here, but additional observations are needed. At 5150 feet (FIG. 8) again an inverse relationship between flowering and flushing seems to be indicated. At 4000 feet (FIG. 10), on the other hand, during the summer of 1971 both flowering and flushing were absent, while in winter 1971-72 flowering reached a peak and flushing was very low. At 3000 feet (FIG. 4) no immediate relationship between flowering and flushing is evident.

Ripe fruits remain on the tree for periods of a year or more and seeds drop throughout the year.

Circumference changes varied from plot to plot. All samples taken indicated cambial activity was in progress. However, on an annual basis, plants at 4000 feet (FIG. 30) increased in circumference about three times as rapidly as those at 3000 feet (FIG. 24), and about five times as rapidly as those at 6700 feet (FIG. 22).

Plants at 5150 feet (FIG. 28) varied widely from month to month, but showed an average decrease in circumference during the year, while plants at 6000 feet (FIG. 40) have also decreased in circumference during the period they have been observed. The environmental factors related to such variation have not yet been determined.

Cheirodendron trigynum. (FIGS. 6, 26)

The 'olapa exhibited definite seasonality of flowering and flushing in the Kilauea Forest Reserve (FIG. 6). Heavy flushing occurred in late winter and spring (January through June) while peak flowering was during the summer (July). In this species inflorescences are produced terminally on new shoots and peak flowering thus follows peak flushing. There seems to be some variability in flowering from year to year as flowering in 1972 was much lower then in 1971 even though the amount of flushing was similar in both years. A few ripe fruits can be observed on the trees throughout the year.

Growth was quite rapid in this species throughout the first year (Fig. 26), but dropped off during the spring of 1972.

Sapindus saponaria. (FIGS. 9, 29)

The manele is deciduous, and flushing, flowering, and leaf fall all show definite seasonal peaks (FIG. 9). Leaf fall occurs between January and May with a peak in February-March. Flushing starts in February and peaks in May. On any one tree most branches are synchronized and all leaves are lost within a month, but heavily shaded branches and sucker shoots typically retain their leaves for a few months longer. Most trees in the plot lose most of their leaves within a two-month period, but leaf fall is protracted because of the lag shown by the shaded and sucker shoots. Flushing begins within one to two months of leaf fall, so any given shoot will be leafless for only one to two months.

Flowers develop terminally on new shoots and peak flowering occurs in late summer and early fall. Fruits ripen in the winter and most drop then, but some persist on the tree for several months.

Circumference data (FIG. 29) indicate that the trees grew fairly rapidly during most of 1971, but there was a decrease in circumference between December 1971 and June 1972.

Diospyros ferrea. (FIGS. 12, 32)

The lama is an evergreen sclerophyll which grows in areas that typically have a summer-drought climate. Peak flowering (FIG. 12) takes place during spring and early summer, with very little flowering in late summer and fall. Peak flushing occurs during the wetter winter months, although some flushing is evident all year round. Some ripe fruits can be found at any month but most fruits ripen and fall during early winter (December-January).

Growth (FIG. 32) appears to be more rapid during wetter months, with lower rates of increase or even decreases in circumference occurring during the summer.

Erythrina sandwicensis. (FIGS. 13, 33)

The wiliwili is deciduous, and flowering, flushing, and leaf fall all show distinct seasonal peaks (FIG. 13). Peak leaf fall occurs in April and May. Flowers develop on old shoots and heavy flowering occurs on leafless branches during the dry season in summer and early fall (July through September). Flushing begins just after flowering, in August and September on early-flowering trees, and peaks about November. Fruits ripen and drop seeds in a few months, but some open fruits containing mature seeds may remain on the tree for a year or more.

Branches which are growing in deep shade and sucker shoots tend to show a lag in phenophase of one to three months behind other shoots.

Circumference changes (FIG. 33) are difficult to interpret. There is a suggestion that growth may be more rapid during the spring, but the data are hardly conclusive on this point.

Ilex anomala. (FIGS. 14, 34)

The kawa'u (FIG. 14) shows peak flowering in late summer (July and August) but the prolonged flowering period continues on through the fall and winter into February. Flushing is also prolonged, starting in December, peaking in April or May, and ending in July. In 1971 there was a second, less extensive, period of flushing from late July through October.

Increases in circumference (FIG. 34) are fairly uniform throughout the year.

Coprosma ochracea (FIGS. 15, 35)

The pilo (FIG. 15) exhibits distinct seasonality in flushing and flowering. In this species flowers develop in axils of newly formed leaves; thus flushing and flowering periods coincide. Flushing and flowering occur from spring through early summer, peaking in April and May. Fruits ripen during the fall and most drop between December and February.

Increases in circumference (FIG. 35) occur relatively uniformly throughout the year.

Myrsine lessertiana. (FIGS. 16, 36)

The kolea (FIG. 16) shows some flushing throughout the year with a pronounced peak in the spring (March to May) and a less pronounced peak in the fall (November). Peak flowering is in spring, extending into summer. This species flowers on older parts of the stem, usually from axils of fallen leaves. Most fruits ripen during the summer.

Increases in circumference (FIG. 36) occur relatively uniformly throughout the year.

Myoporum sandwicense. (FIGS. 17, 37)

The naio (FIG. 17) does not seem to exhibit pronounced seasonality in flushing, but appears to undergo vegetative growth throughout the year. The flowering period is prolonged, starting in May and extending to December or January with a peak probably in late summer and fall. Some ripe fruits can be found at any month of the year.

Changes in circumference (FIG. 37) vary from month to month but no pattern is yet evident.

Santalum ellipticum. (FIGS. 18, 38)

The iliahi has been observed only from October to June, but has exhibited both flowers and new flushes during all this period. Flowers form at the tips of new flushes and the flowering curve (FIG. 18) appears to lag behind the flushing curve by about a month. Both flowering and flushing occurred at somewhat lower levels during the winter and early spring.

Changes in circumference which have been observed (FIG. 38) are so varied that we cannot yet interpret them.

Dodonaea viscosa. (FIGS. 21, 41)

The 'a'ali'i has been studied for less than one year, but flowering (FIG. 21) does not appear to be seasonal. Plants were in full flower in November, and flowering continued at a relatively high level through March, dropping off sharply thereafter. Flushing was evident at all months, but was highest during March through May when flowering activity was decreasing. Ripe fruits can be found throughout the year.

During the early stages of flowering this population seemed to be strictly dioecious, with staminate flowers on some trees and pistillate flowers on others. However, it was noted that "staminate" plants bore a few fruits formed during the previous flowering season. The reason for this became evident when the "staminate" plants were found to form a few perfect flowers toward the end of the flowering period.

Circumference changes (FIG. 41) cannot yet be interpreted.

Extensive studies

Although observations have been made on more than 70 species (TABLE 3), not all of these have been studied for a full year, and others do not show patterns greatly different from those described above. This, in this preliminary report data will be presented for only a few selected species.

Pteridium aquilinum.

This fern was studied in plots 1, 2, 3, 5, 6, and 8. In plots 5, 6, and 8, at elevations from 3000 to 4000 feet, new fronds were produced regularly throughout the year. In plot 3, at 5150 feet, new fronds were produced from February through July. By December most fronds had died and turned brown but a few remained green and living throughout the winter. In plot 2 at 6000 feet new fronds were produced from February through April, and most had died by December, although a few lived throughout the winter. In plot 1 at 6700 feet new fronds were produced from March through May, and most were dead by October. No green fronds were found during the winter. Thus, seasonal behavior occurs at higher elevations while at lower elevations the plants are not seasonal. This suggests that seasonality may be related to temperature in this species.

Hypochaeris radicata.

This introduced weedy herb was studied in plots 1, 2, 3, 4, 6, 7, and 8. In all plots it was found flowering during all months.

Styphelia tameiameiae.

This shrub was studied in plots 1, 2, 3, 6, and 8. In all plots it was found with new flushes, with flowers, and with immature and mature fruits at all months.

Coprosma rhynchocarpa.

This tree, studied in plot 5, showed essentially the same timing in its phenophases as Coprosma ochracea, discussed above. The two species grow at similar elevations, are morphologically similar, both small understory trees, but C. rhynchocarpa occurs in the summer-dry area of Kipuka Puaulu while C. ochracea was studied in the humid montane rain forest at Thurston Lava Tube.

DISCUSSION

Phenology

The results to date indicate that most species studied exhibit some seasonality in flushing, flowering, fruiting, and (in deciduous species, at least) leaf fall. Most phenophases show single annual peaks, although the timing of these peaks may differ from one year to the next (see, e.g., flowering in Cheirodendron, FIG. 6).

As is characteristic of many species in the humid tropics, the duration of various phenophases generally extends over periods of several months. Similarly, the onset and cessation of most phenophases is gradual, rather than sharply marked.

While the use of such terms as summer and winter to categorize seasons in Hawaii is not especially accurate, it is convenient to use these terms to describe timing of phenophases. Since most phenophases extend over periods of several months it would be cumbersome to name all the months in a discussion. Therefore, winter is used in this paper to refer to December through February, spring for March through May, summer for June through August, and fall for September through November.

A detailed analysis of relationships between various environmental factors and seasonal behavior of plant species will not be attempted until further data are available. However, a few generalizations can be made.

A. In many species, the major period of seed drop is during the fall or winter, i.e., during a time of heavier rainfall.

B. Peak flowering times can be categorized as follows (flowering may begin in the preceding season and/or extend to the following season but peak flowering occurs during the season indicated):

a) Species with peak flowering in winter:

Sophora chrysophylla at 4000 and 5150 feet. At 6000 and 6700 feet peak flowering occurs in winter but some flowering occurs throughout most of the year.

Acacia koa at 4000, 5150, 6000, and 6700 feet. At 5400 feet in the Kilauea Forest Reserve peak flowering was in October but the flowering period extended from September to March and was high during the winter.

b) Species with peak flowering in spring:

Diospyros ferrea

Coprosma ochracea

Myrsine lessertiana

c) Species with peak flowering in summer:

Cheirodendron trigynum

Sapindus saponaria

Erythrina sandwicensis

Ilex anomala - extending into fall and winter.

Myoporum sandwicense - extending into fall.

Santalum ellipticum - extending into fall.

d) Species with peak flowering in fall:

Dodonaea viscosa - extending into winter and spring.

e) Species without pronounced flowering peak:

Sophora chrysophylla (at 3000 feet only).

C. Time of peak vegetative flush can be categorized as follows:

a) Species with peak flush in winter:

Acacia koa (at 4000 feet only) - starting in fall, extending into spring.

Cheirodendron trigynum - heavy flush extending into spring.

Diospyros ferrea - heavy flush starting in fall.

b) Species with peak flush in spring:

Sophora chrysophylla at 6000 feet; at 4000 feet peak flushing in spring with a second flush in fall.

Acacia koa at 5150 feet; at 4500 and 6000 feet peak flush in spring with heavy flush extending into summer.

Sapindus saponaria

Ilex anomala

Coprosma ochracea

Myrsine sandwicensis

c) Species with peak flush in summer:

Sophora chrysophylla at 5150 and 6700 feet, in both places with heavy flush in spring but peak in summer.

Acacia koa (at 6700 feet only).

Santalum ellipticum - heavy flush extending into fall

d) Species with peak flush in fall

Erythrina sandwicensis, heavy flush extending into winter.

e) Species without pronounced flushing peak:

Sophora chrysophylla (at 3000 feet only).

Myoporum sandwicense

Dodonaea viscosa (Probably, but a full year of observations have not yet been completed).

Growth

Although all cambial samples collected have exhibited evidence of activity in the vascular cambium as shown by slipping of the bark at time of sampling, it has not yet been possible to quantify the amount of cambial activity. We hope to have sufficient data to do so in another year.

Circumference data (FIGS. 22-41) show that monthly changes occur in circumference of all species studied. However, we have been unable to demonstrate significant correlations between these rates of change in circumference (reflecting different rates of growth in stems) and environmental factors.

Analyses of rainfall/growth relationships have been made. Weekly rainfall records were available from five stations. The National Park Service provided records from the top of the Mauna Loa Strip Road (6700 feet, in plot 1), Park Headquarters (4000 feet, near plots 5, 6, and 7), and Kalapana No. 1 (near plot 9). IBP data were available from the Mauna Loa Strip Road (5350 feet, near plots 2, 3, and 5), and from the Kilauea Forest Reserve (5400 feet, in plot 4). Monthly rainfall totals from each station are shown in FIGS. 42-46.

In an effort to determine any relationships between growth rates (as indicated by circumference changes) and rainfall, total rainfall in the 1 week, 2 week, 2 week, 4 week, 6 week, 8 week, and 12 week periods preceding each observation date were determined. Linear regression analyses were made between the growth rate (expressed as average daily change in μm for the period between two consecutive observation dates, and the rainfall (in mm) for each of the six periods preceding the second observation date.

When a plot was not close to a rainfall station, analyses were made using rainfall data for the two closest available stations.

The correlation coefficients from the linear regression analyses are given in TABLE 4. Very few significant correlations between growth and rainfall were found, FIGS. 42 - 46. Monthly rainfall totals at weather stations closest to study plots. Rainfall data for February 1972 are not available for the 6700 feet, Strip Road station (FIG. 42).

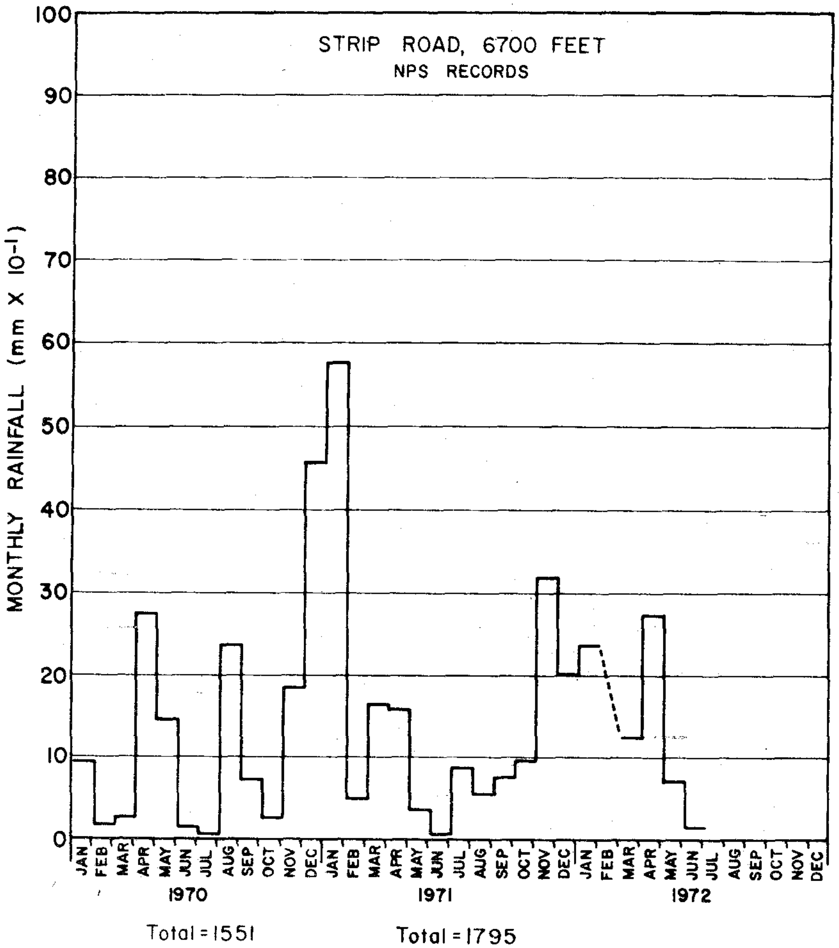

STRIP ROAD, 6700 FEET
NPS RECORDS
MONTHLY RAINFALL (mm X 10⁻¹)
0 10 20 30 40 50 60 70 80 90 100
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1970
1971
1972
Total = 1551
Total = 1795

FIG. 42

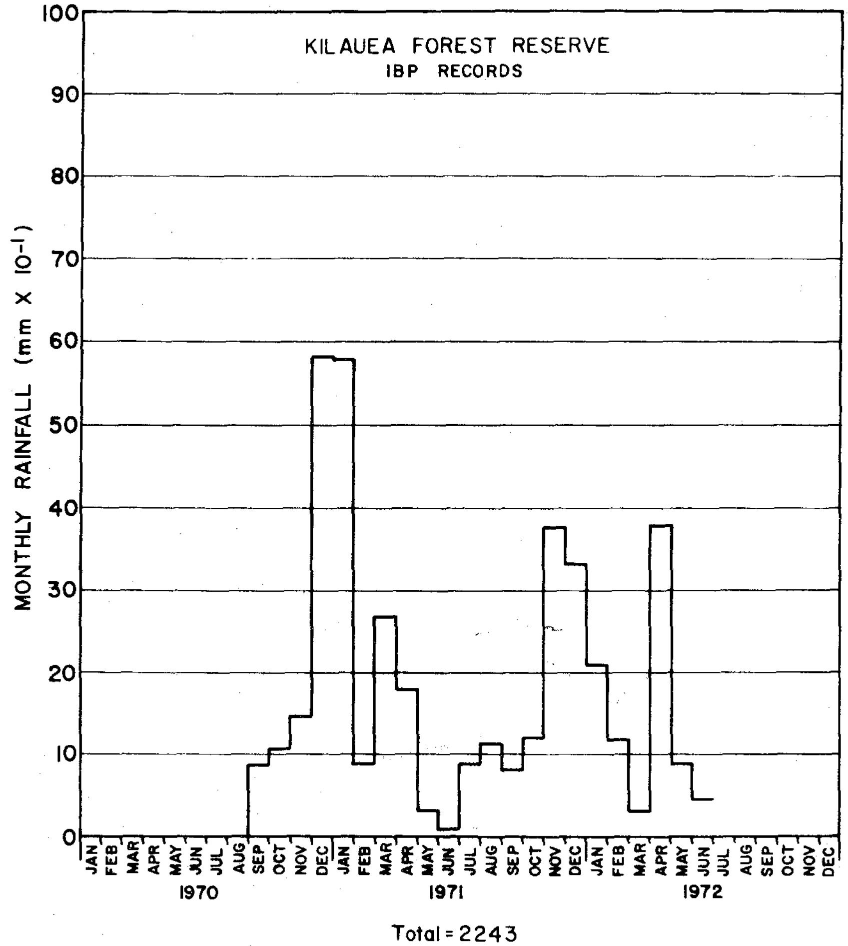

KILAUEA FOREST RESERVE
IBP RECORDS
MONTHLY RAINFALL (mm X 10⁻¹)
0 10 20 30 40 50 60 70 80 90 100
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1970
1971
1972
Total = 2243

FIG. 43

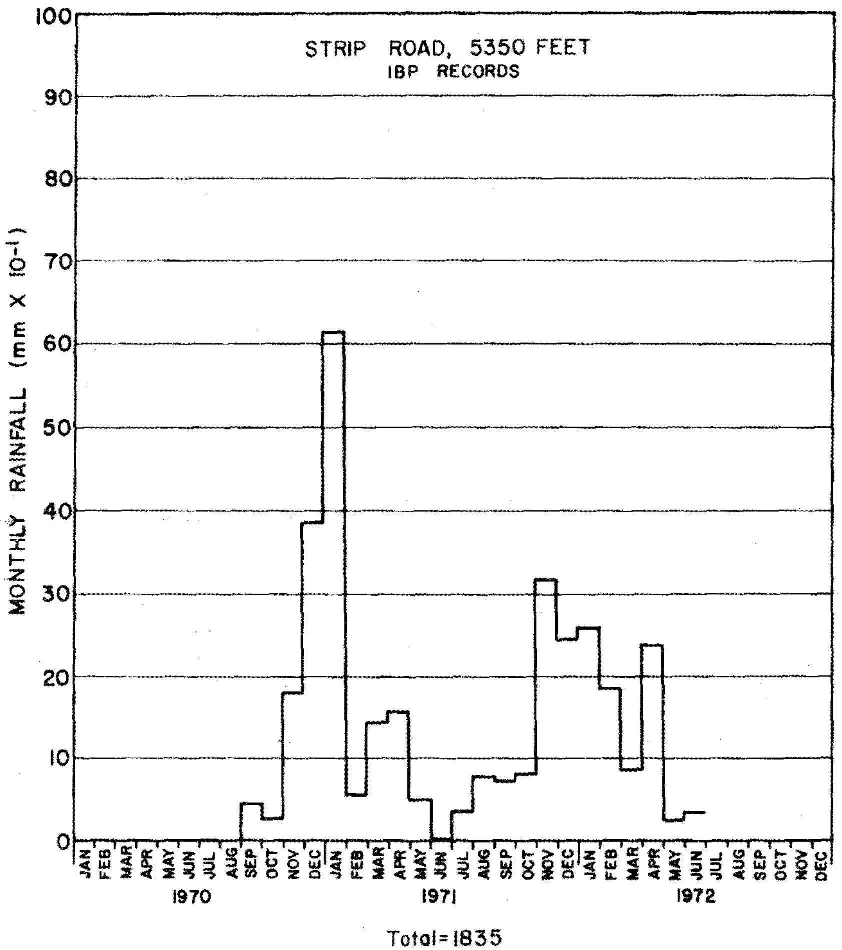

STRIP ROAD, 5350 FEET
IBP RECORDS
MONTHLY RAINFALL (mm X 10⁻¹)
0
10
20
30
40
50
60
70
80
90
100
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1970
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1972
Total=1835

FIG. 44

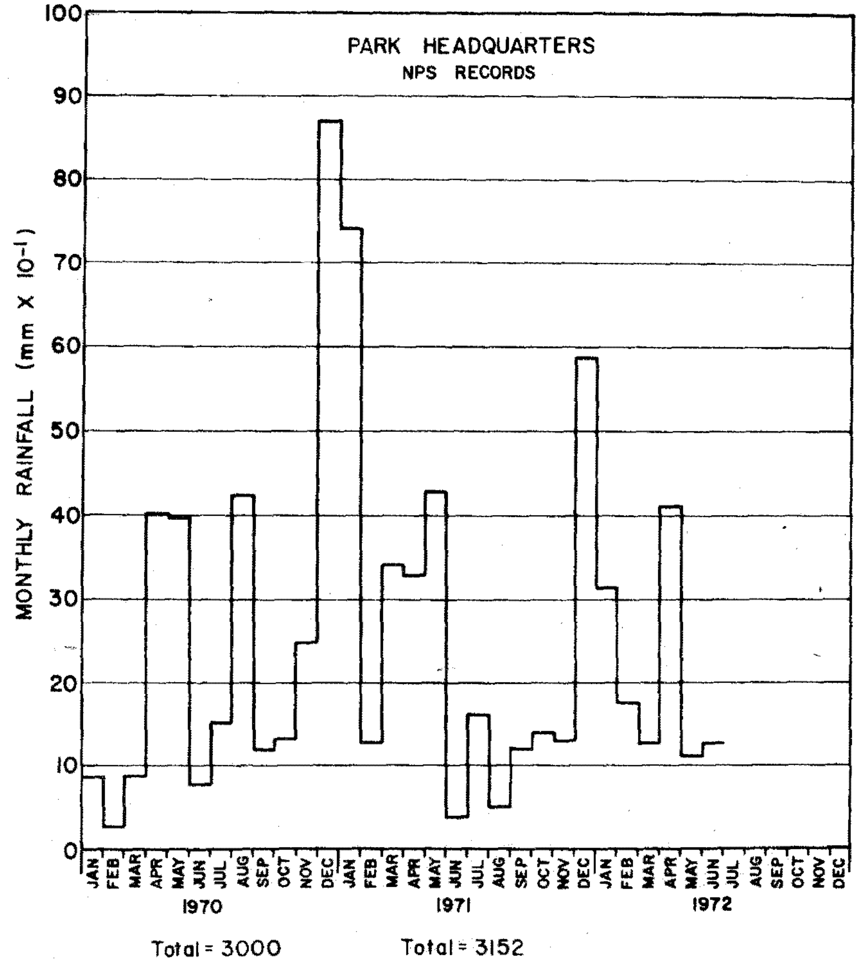
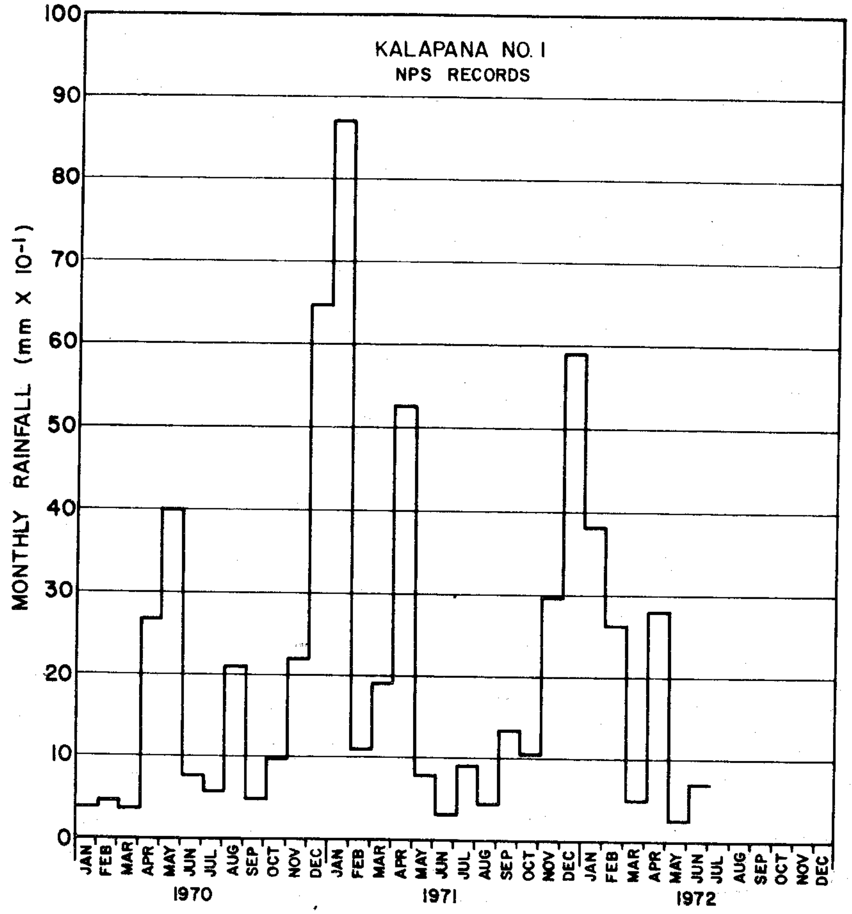

PARK HEADQUARTERS
NPS RECORDS
MONTHLY RAINFALL (mm X 10⁻¹)
0
10
20
30
40
50
60
70
80
90
100
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1970
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1971
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1972
Total = 3000
Total = 3152

FIG. 45



Total=2129 Total=3031

FIG. 46

TABLE 4. Correlation coefficients from linear regression analyses. Growth (μm/day) vs. rainfall (mm). * = $p > .05$, ** = $p > .01$

Rainfall, no. of weeks prior to growth measurements (Plants/ Plot no.)	Sophora Plot 1 RF on site	Acacia Plot 1 RF on site	Sophora Plot 8 RF at Park Headquarters	Cheirodendron Plot 4 RF on site	Acacia Plot 4 RF on site
1	.057	.412	.299	-.271	-.515
2	.488	-.076	.219	-.357	-.376
3	.670	-.257	.083	-.216	-.159
4	.910*	-.324	-.344	-.353	-.157
6	.786	-.545	-.330	-.583	-.239
8	.538	.389	-.193	-.607*	-.245
12	.976*	.726	.022	-.569	-.346
			RF at Kalapana No. 1		
1			.161		
2			.108		
3			.011		
4			-.239		
6			-.151		
8			-.098		
12			.073		

TABLE 4. Continued.

Rainfall, no. of weeks prior to growth measurements — Plants/ Plot no.	Acacia Plot 3	Sophora Plot 3	Sapindus Plot 5	Sophora Plot 5	Acacia Plot 5
	RF 5350 ft.	RF 5350 ft.	RF Park Headquarters	RF Park Headquarters	RF Park Headquarters
1	.201	.823**	.360	.460	-.142
2	-.208	.564	.225	.339	-.280
3	-.248	.379	.334	.471	-.061
4	-.141	.158	-.167	-.015	-.216
6	-.049	.148	-.267	-.021	-.192
8	.107	.145	-.401	-.064	-.243
12	-.065	-.014	-.595	-.332	-.511
			RF 5350 ft.	RF 5350 ft.	RF 5350 ft.
1			.421	.533	-.029
2			.548	-.067	-.473
3			.489	-.276	-.573
4			.227	-.450	-.654*
6			.048	-.388	-.641*
8			-.046	-.339	-.585
12			-.299	-.424	-.786**

TABLE 4. Continued.

Rainfall, no. of weeks prior to growth measurements / Plants/ Plot No.	*Diospyros* Plot 9 RF on site	*Erythrina* Plot 9 RF on site	*Ilex* Plot 7 RF Park Headquarters	*Coprosma* Plot 7 RF Park Headquarters	*Myrsine* Plot 7 RF Park Headquarters
1	.295	.037	.310	.008	.306
2	.265	.140	.074	.003	.280
3	.224	.149	.332	-.076	.372
4	-.031	.092	.013	-.262	-.094
6	.133	.106	-.114	-.349	-.195
8	.133	.128	-.328	-.459	-.360
12	.307	.430	-.634*	-.189	-.381

TABLE 4. Concluded.

Rainfall, no. of weeks prior to growth measurements — Plants/Plot No.	*Myoporum* Plot 4	*Santalum* Plot 6	*Acacia* Plot 2	*Sophora* Plot 2	*Dodonaea* Plot 3
	RF on site	RF Park Headquarters	RF 5350 ft.	RF 5350 ft.	RF 5350 ft.
1	.721	.281	.760	-.385	-.087
2	.537	.316	.804	-.202	.417
3	.330	.378	.458	.041	.450
4	.451	.213	.140	.537	.342
6	.448	.116	.131	.637	.492
8	.612	.033	.213	.905*	.307
12	.406	-.408	.183	.668	-.164

and their distribution in the table creates some doubt that these are more than chance correlations. For example, there is a significant correlation between 4-week rainfall and Sophora growth in plot 1 and a significant correlation between 12-week rainfall and Sophora growth in the same plot. Yet correlations between 1-, 2-, 3-, 6-, and 8-week rainfall and Sophora growth were not significant. In view of such results, it appears that we have not been able to demonstrate any clear relationships between rainfall and growth in our plots.

Average annual growth rates have been determined for all species studied for at least one year. These values are indicated by the dashed horizontal lines in FIGS. 22-36. They indicate differences among species and differences within the same species growing in different plots. At this time we do not have sufficient information on climatic and edaphic factors to interpret these differences.

Although our data suggest that rainfall, as such, seems not to be correlated directly with growth rates of the trees measured in our plots, it still seems worthwhile to search for some relationship between moisture and growth rate. One parameter which has not yet been examined is soil moisture, another is fog drip.

Still other parameters which would provide useful information are incoming solar radiation and temperature. We hope that such data will be obtained during the course of the Hawaii IBP project, as it appears that without them we will not be able to understand the relationships between environmental factors and growth in these ecosystems.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Miss Lynn Matsunami for her technical assistance in all aspects of this study; to Dr. John Porter for his assistance in establishing some of the plots and his help in collecting data; and to Mr. James Jacobi for his help in collecting data. FIGS. 2-21 were prepared by Mr. Tamotsu Nakata; all other figures by Mr. Charles Bretz.

LITERATURE CITED

BAKER, J. R. and I. BAKER. 1936. The seasons in a tropical rainforest (New Hebrides). Part 2. Botany. J. Linn. Soc. (Zool.) 39:507-519.

BALDWIN, P.H. 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves: Drepanididae). U. Calif. Publ. Zool. 52:285-398.

BLUMENSTOCK, D. I. and S. PRICE. 1967. Climates of the states. Hawaii. U. S. Dept. Commerce. E.S.S.A. Climatography U. S. No. 60-51. 27 pp.

BROWN, F. B. H. 1922. The secondary xylem of Hawaiian trees. B. P. Bishop Mus., Occas. Pap. 8(6):157 pp.

CHOWDHURY, K. A. 1939. The formation of growth rings in Indian trees. I. (a)chir (b) cutch (c) jaman (d) laurel (e) sal (f) semul (g) teak. Indian For. Records (n.s.) Utilization. 2:1-40.

CHOWDHURY, K. A. 1940a. The formation of growth rings in Indian trees. II. (a)champ (b) kokko (c) sisso (d) toon. Indian For. Records (n.s.) Utilization. 2:41-58.

CHOWDHURY, K. A. 1940b. The formation of growth rings in Indian trees. III. A study of the effect of locality. Indian For. Records (n.s.) Utilization. 2:59-75.

CHOWDHURY, K. A. and S. S. GHOSH. 1950. Formation of growth rings in Indian trees. V. Study of some discs of sandalwood (Santalum album). Indian For. Records (n.s.) Botany 11:16.

CHOWDHURY, K. A. and K. R. RAO. 1949. Formation of growth rings in Indian trees. IV. False rings in saplings of teak (Tectona grandis) and mahogany (Swietenia macrophylla). Indian For. Records (n.s.) Botany 11:1.

COSTER, C. 1923. Laubererneuerung und andere periodische Lebenprozesse in dem trockenen Monsun-Gebier Ost-Javas. Ann. Jard. Bot. Buitenzorg 33:117-189.

COSTER, C. 1925. Die Fettumwandlung im Baumkörper in den Tropen. Ann. Jard. Bot. Buitenzorg 35:71-104.

COSTER, C. 1926. Periodische Blüteerscheinungen in den Tropen. Ann. Jard. Bot. Buitenzorg 35:125-162.

COSTER, C. 1927. Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. Ann. Jard. Bot. Buitenzorg 37:49-160.

COSTER, C. 1928. Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen (cont.). Ann. Jard. Bot. Buitenzorg 38:1-114.

DAUBENMIRE, R. 1972. Phenology and other characteristics of tropical semideciduous forest in north-western Costa Rica. J. Ecol. 60:147-170.

HOLTTUM, R. E. 1940. On periodic leaf-change and flowering of trees in Singapore. II. Garden's Bull. Straits Settlement. 11:119-175.

KORIBA, K. 1958. On the periodicity of tree growth in the tropics with reference to the mode of branching, the leaf fall, and the formation of the resting bud. Garden's Bull. Straits Settlement 17:11-81.

LAMBERTON, A. R. H. 1955. The anatomy of some woods utilized by the ancient Hawaiians. M.S. thesis, Univ. Hawaii, Honolulu.

LANNER, R. M. 1965. Phenology of Acacia koa on Mauna Loa, Hawaii. Pac. S.W. For. and Range Exp. Sta., U. S. For. Serv. Res. Note PSW-89. 9 pp.

LANNER, R. M. 1966. The phenology and growth habits of pines in Hawaii. Pac. S.W. For. and Range Exp. Sta., U. S. For. Serv. Res. Paper PSW-29. 25 pp.

MARIAUX, A. 1967. Les cernes dans les bois tropicaux africains, nature et periodicité. Peuvent-ils révéler l'age des arbres? Bois Forêts Trop. 113:3-14: 114:23-37.

McCLURE, H. E. 1966. Flowering, fruiting and animals in the canopy of a tropical rain forest. Malay For. 29:182-203.

NEAL, M. C. 1965. In gardens of Hawaii. B. P. Bishop Mus. Spec. Pub. 50. 924 pp.

NJOKU, E. 1963. Seasonal periodicity in the growth and development of some forest trees. I. Observations on mature trees. J. Ecol. 51:617-624.

PEARSALL, G. 1951. The phenology of ornamental plants in the Honolulu area. M.S. thesis, Univ. Hawaii, Honolulu.

PINTO, A. E. 1970. Phenological studies of trees at El Verde. In: H. T. Odum, ed. A tropical rain forest, a study of irradiation and ecology at El Verde, Puerto Rico. U.S.A.E.C. TID-24270. pp. D-237-D-269.

PORTER, J. R. 1972. The growth and phenology of Metrosideros in Hawaii. Ph. D. dissertation, Univ. Hawaii, Honolulu. 291 pp.

RASID, R. 1963. Phenology and floral ontogeny of the skunk tree, Sterculia foetida Linnaeus. M.S. thesis, Univ. Hawaii, Honolulu. 77 pp.

RICHARDS, P. W. 1964. The tropical rain forest. Cambridge Univ. Press. 450 pp.

ROCK, J. F. 1913. The indigenous trees of the Hawaiian Islands. Honolulu. 518 pp.

SASTRAPRADJA, D. S. and C. H. LAMOUREUX. 1969. Variations in wood anatomy in Hawaiian Metrosideros (Myrtaceae). Ann. Bogoriensis 5:1-83.

STUDHALTER, R. A. 1955. Tree growth. I. Some historical chapters. Bot. Rev. 21:1-72.

STUDHALTER, R. A., W. S. GLOCK, and S. R. AGERTER. 1963. Tree growth. Some historical chapters in the study of diameter growth. Bot. Rev. 29:245-365.

WOLTER, K. E. 1968. A note on a new method for marking xylem growth. For. Sci. 14:102-104.